# Predicted sensory consequences of voluntary actions modulate amplitude of preceding readiness potentials

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## ARTICLE INFO

## ABSTRACT

Self-generated, voluntary actions, are preceded by a slow negativity in the scalp electroencephalography (EEG) signal recorded from frontal regions (termed 'readiness potential'; RP). This signal, and its lateralized sub-component (LRP), is mainly regarded as preparatory motor activity associated with the forthcoming voluntary motor act. However, it is not clear whether this neural signature is associated with preparatory motor activity, expectation of its associated sensory consequences, or both. Here we recorded EEG data from 14 healthy subjects while they performed self-paced button presses with their right index and middle fingers. Button-presses with one finger triggered a sound (motor + sound condition), while button-presses with the other finger did not (motor-only condition). Additionally, subjects listened to externally-generated sounds delivered in expected timings (sound-only condition). We found that the RP amplitude (locked to time of button press) was significantly more negative in the motor + sound compared with motor-only conditions. Importantly, no signal negativity was observed prior to expected sound delivery in the sound-only condition. Thus, the differences in RP amplitude between motor + sound and motor-only conditions are beyond differences in mere expectation of a forthcoming auditory sound. Our results suggest that information regarding expected auditory consequences is represented in the RP preceding voluntary action execution.

## 1. Introduction

Self-generated, voluntary actions are rarely performed without a preceding preparation or planning period during which various decisions regarding the upcoming actions' time, trajectory and goal are made. Accumulating research over the past decades suggests that neural activity during the time interval preceding voluntary action execution is associated with different aspects of the forthcoming motor act, such as task, action type, and selection of the appropriate effector (Haggard, 2008). This view is supported by functional magnetic resonance imaging (fMRI) and electrophysiological studies in humans and primates showing that the neural activity during preparatory time intervals preceding action execution can represent, for example, the type of actions (grasping or touching; Gallivan et al., 2011), the executing effector (right or left hand; Soon et al., 2008) or the tool that is about to be used (Brandi et al., 2014; see also Bulea et al., 2014; Cisek and Kalaska, 2004; Perez et al., 2015)

Self-initiated, voluntary actions are usually preceded by a slow negativity in the scalp electroencephalography (EEG) recorded from frontal and central regions (termed "readiness potential", RP;

Kornhuber and Deecke, 1990; Libet et al., 1983). This negativity, is usually divided into early and late phases, starting around ~1500 ms and ~500 ms prior to action execution, respectively (Shibasaki and Hallett, 2006). The early phase is believed to reflect gradual increase in neural firing rate in high motor cortical regions such as supplementary motor area (SMA) and are associated with preparation and initiation of the forthcoming motor act (Lang et al., 1991; Yazawa et al., 2000; Fried et al., 2011; Pedersen et al., 1998; Cunnington et al., 2003). The late phase is more lateralized and specific to the motor command of the executing effector and is therefore believed to represent preparatory activity in primary motor cortex (M1; Passingham, 1987; Pedersen et al., 1998).

When an unimanual voluntary action is performed, for example, by a right hand, stronger negativity is usually found over the left hemisphere - contralateral to the active hand (Kutas and Donchin, 1980). This difference in RP has been shown to begin in close temporal proximity to initiation of the motor act (De Jong et al., 1988; Gratton et al., 1988; Smid et al., 1987) and is usually detected by subtracting the RP signal over the ipsilateral hemisphere from that of the contralateral hemisphere with respect to the active hand. This late RP
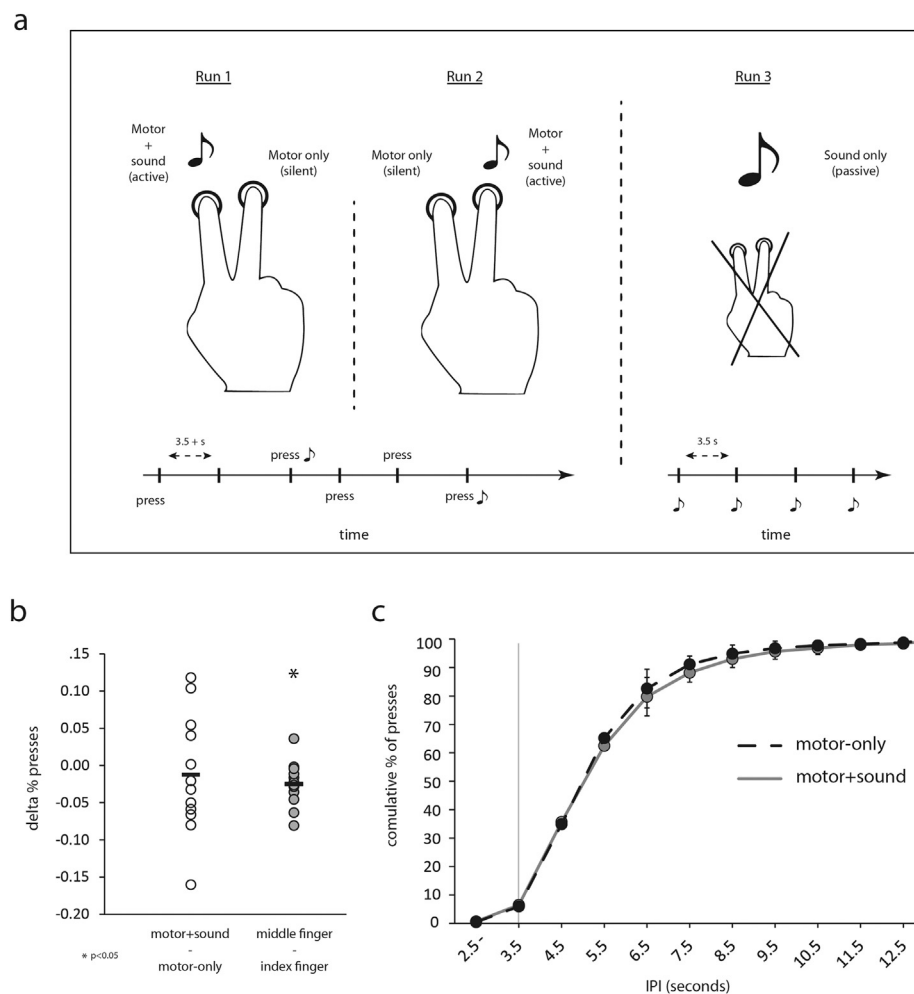
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Fig. 1. Experimental design and behavioral results. (a) The experiment consisted of three runs. In the first two runs, subjects performed voluntary self-paced button presses with their index and middle fingers. In one run, index finger presses triggered auditory stimuli (motor + sound condition), while middle finger presses did not (motor-only condition; Run 1 in the Figure). In the other run, the finger mapping was reversed, such that middle finger presses triggered auditory stimuli and index finger presses did not (Run 2 in the Figure). The order of runs 1 and 2 was counterbalanced across subjects. After the two runs, subjects listened to externally-generated auditory stimuli delivered at a fixed rate (Run 3 in the Figure). (b) Scatter plots depicting individual subjects' differences between proportion of motor + sound and motor-only trials (hollow circles) and between proportion of middle finger and index finger presses (filled circles) out of the total number of trials for each subject. The black bars denote group average. Proportion of motor + sound and motor-only trials was not significantly different across subjects; however, subjects pressed more frequently with their index compared with middle fingers (p = 0.03). (d) Cumulative distribution of inter-press-intervals across subjects in motor + sound and motor-only condition was not significantly different. The vertical line denotes lowest IPI limit for definition of "good" trials taken for analysis. Each data point denotes mean ± st.d. across subjects, percentage of presses with lower IPI (total of 12 time bins; repeated measures ANOVA, n.s.).

component, termed the lateralized readiness potential (LRP), is interpreted as manifestation of preparatory brain activity that is more specific to the executing effector which is about to perform the action.

Despite recent evidence suggesting that RP does not necessarily reflect motor preparation, but might be associated with general decision making processes (Alexander et al., 2016), this neural signature is predominantly discussed in the framework of a neural correlate of motor intention and consciousness of such intention (Haggard and Eimer, 1999; Libet et al., 1983). Nevertheless, the link between RP and self-generated sensory consequences can be formulated within the forward model of sensory-motor integration (Wolpert et al., 1995). According to the model, during the preparatory period prior to voluntary action execution, the motor cortex sends signals both to the executing effectors and to the relevant sensory cortex, in which the sensory consequences of the action are expected. The signal that is sent from motor to sensory cortices was termed "efference copy" (von Holst, 1954) and was proposed to facilitate, attenuate, or otherwise modulate both perceptual and neural responses to self-generated stimuli compared with responses to identical stimuli generated by an external source (Crapse and Sommer, 2008). Therefore, the RP and its LRP subcomponent, are candidate neurophysiological signatures for such a forward model embedding the expected sensory consequences of self-generated actions.

The aim of the current study was to examine whether the RP and/or LRP encode the expected sensory consequences triggered by voluntary actions. To this end, we recorded EEG data from healthy subjects while they performed voluntary, self-paced button presses either with or without expected auditory consequences.

## 2. Materials and methods

### 2.1. Subjects

Fourteen healthy, right-handed undergraduate students naïve to the purposes of the study were recruited to the experiment (four males; mean age: 23, rage: 19–26 years). The study conformed to the guidelines that were approved by the ethical committee of Tel-Aviv University. All subjects provided written informed consent to participate in the study and were compensated for their time.

### 2.2. Procedure

Subjects were seated in a dimly lit room and performed self-paced button presses with index or middle fingers of their right hand while fixating on a cross ("+") constantly displayed on a computer screen. The task consisted of two consecutive runs - in one run, middle finger button-presses triggered an auditory stimulus (300 ms C major piano chord generated by MIDI-OX software ver. 7.0.2, delivered through free field speakers; motor + sound condition), while index finger button-presses did not trigger any auditory stimulus (motor-only condition); in the other run, the finger mapping with respect to sound was reversed (middle finger button press = motor-only condition; index finger button press = motor + sound condition). The order of runs (finger-mapping) was counterbalanced across subjects. Before the experimental procedure, subjects were informed about the finger-sound mapping and were instructed to perform the button presses in a self-paced manner (with at least 3–4 s between consecutive presses), freely choosing

between index and middle finger. If inter press interval (IPI) of two consecutive presses was less than 3.5 s, the fixation point changed its color to red for 500 ms to inform the subject of insufficient IPI and the data related to the last button-press were discarded from analysis. Each run ended when subjects performed at least 70 "good" presses (with IPI greater than 3.5 s) with each finger.

To allow detection of brain activity evoked by mere expectation of auditory stimuli (without a motor component), subjects underwent an additional run, during which they listened to externally-generated repetitions (n = 70) of the same chord presented in the motor + sound condition, delivered in a fixed rate of once every 3.5 s (sound-only condition; Fig. 1a). In order to keep subjects engaged during this run, they performed an oddball detection task (300 ms, 500 Hz pure tone; additional ten pseudo-randomly interspersed odd-ball trials per run). Detection of such oddballs was reported by a button press and data from these catch trials was not analyzed.

### 2.3. EEG recording and data analysis

EEG signals were recorded using a BIOSEMI Active II 64-channel system at a sampling rate of 256 Hz. Additional 3 channels were used to record activity related to ocular artifacts and 2 more channels placed on right and left mastoids served as offline reference channels.

The EEG data was analyzed using Matlab (2013b; MathWorks) and EEGLAB toolbox (version 12.0.1). The continuous data was re-referenced to the average of the mastoid channels and off-line filtered with a Hamming windowed finite impulse response 0.05–40 Hz band pass filter with the order of 16896 implemented in EEGLAB toolbox (function pop_eegfiltnew). We segmented the data into epochs covering the time window from -2.6 to 0.6 s relative to trial onset (time 0; a button press in the motor + sound and motor-only conditions, and sound delivery in the sound-only condition). For removing ocular artifacts, we used independent component analysis (ICA) implemented in EEGLAB toolbox. Ocular ICA components (range across subjects: 1–2 components) were identified by visual inspection and deleted from the global signal. Noisy trial epochs (exceeding $\pm$ 100 μV range) at Fz, FCz, Cz, C3 and C4 channels were identified in the raw data and rejected from the analysis. Finally, for each subject the number of trials in motor-only, motor + sound and sound-only conditions was balanced by taking the first number of trials matching the condition with the lowest number of trials remaining after pre-processing.

Pre-stimulus event related potentials (ERPs) were analyzed at Fz, FCz, Cz, C3 and C4 channels using a baseline period from −2600 ms to −2500 ms (Haggard and Eimer, 1999), relative to event onset. Lateralized readiness potential (LRP; Gratton et al., 1988) was measured by calculating the difference between readiness potentials recorded from C3 and C4 channels (C3 - C4; Smulders et al., 2012). For estimating RP amplitudes, for each subject we calculated the mean signal across trials during the time window from -2500 to 0 ms prior to button press. For estimating LRP amplitudes, we calculated the mean signal across trials during the time window from -500 to 0 ms prior to button press.

## 3. Results

Two subjects were excluded from the analysis since they did not exhibit a negative trend in voltage (readiness potential) prior to movement onset both in motor + sound and motor-only conditions. Similar exclusion rates due to lack of RP have been previously reported (Schurger et al., 2012). All further analyses were conducted on the remaining 12 subjects.

At the behavioral level, there was no significant difference between the proportion of times subjects performed button presses that were associated or not with a sound (median proportion $\pm$ semi interquartile range [SIR] of presses across subjects - motor + sound: 49 $\pm$ 3.29%, motor-only: 51 $\pm$ 3.29%; Wilcoxon test, n = 12, z = -0.266, p = 0.78; Fig. 1b). Subjects did however use more frequently their index finger

compared with middle finger (index finger: 52 $\pm$ 0.60%, middle finger: 48 $\pm$ 0.60%; Wilcoxon test, z = -2.12, p = 0.03; Fig. 1b). Next, we calculated the distribution of inter-press-intervals for the motor + sound and motor-only conditions. We found no significant difference in the distribution of inter-press-intervals (IPI; binned into 12 time intervals) across subjects for the two conditions (repeated measures analysis of variance – condition X time bins, Greenhouse-Geisser corrected $F_{(4,44)} = 2.07$, p = 0.10; main effect of condition, $F_{(1,11)} = 0.256$, p = 0.63; Fig. 1c). The median IPI across subjects was not significantly different between motor + sound and motor-only conditions (motor + sound: 5.00 $\pm$ 0.59 s, motor-only: 4.87 $\pm$ 0.46 s; Wilcoxon test, z = -1.80, p = 0.07). The median $\pm$ SIR percentage of discarded trials (with IPI less than 3.5 s) across subjects was 6.76 $\pm$ 1.73% with no significant difference between motor + sound and motor-only conditions (motor + sound: 6.97 $\pm$ 2.29%, motor-only: 7.39 $\pm$ 2.43%, Wilcoxon test, z = -0.62, p = 0.52). The mean number of balanced trials across subjects that were eventually included in the analysis after preprocessing was 66 (range: 62–70 trials). Subjects had perfect performance in the odd-ball trials detection task in the sound-only condition.

At the physiological level we first examined the differences in the mean RP amplitude across Fz, FCz, Cz channels during the epoch preceding button presses in motor + sound and motor-only conditions. We found that the mean RP amplitude was more negative before motor + sound compared with motor-only conditions (mean $\pm$ s.e.m μV across subjects – motor + sound condition: -1.69 $\pm$ 0.30 μV, motor-only condition: -0.68 $\pm$ 0.35 μV, paired two-tailed $t$-test, $t_{(11)} = 2.36$, p = 0.037; Fig. 2a). This effect was present in 10 out of 12 subjects. Importantly, the EEG signal preceding sound onset in the sound-only condition was not significantly different than zero (mean $\pm$ s.e.m μV across subjects – sound-only condition: 0.14 $\pm$ 0.48 μV, two-tailed $t$-test for sample mean, $t_{(11)} = 0.27$, p = 0.78). Moreover, we found that the mean RP amplitude in the motor + sound condition remained significantly more negative compared with the motor-only condition even after taking into account the EEG signal associated with pure auditory expectancy during sound-only condition (repeated-measures analysis of covariance; $F_{(1,10)} = 6.13$, p = 0.033). Thus, the stronger negativity preceding the motor + sound compared with motor-only conditions is unlikely to be related to mere expectancy of a forthcoming auditory stimulus. To further examine the difference in RP amplitude between motor + sound and motor-only conditions, we performed a Bayesian factor analysis. Using Bayesian information criterion (BIC; Schwarz, 1978), we found that the approximation of the Bayes factor comparing the differences in RP amplitudes was 3.37, thus providing substantial support to the claim that RP amplitude between motor + sound and motor-only conditions is different (Kass and Raftery, 1995).

To examine the involvement of specific RP components in coding expected auditory action consequences, we also examined the lateralized readiness potentials (LRP) preceding motor + sound and motor-only conditions. We found that the mean LRP amplitude preceding motor + sound condition was not significantly different from LRP amplitude preceding motor-only condition (mean $\pm$ s.e.m μV across subjects – motor + sound condition: -1.92 $\pm$ 0.29 μV, motor-only condition: -1.54 $\pm$ 0.30 μV, paired two-tailed $t$-test, t(11) = 1.48, p = 0.16; Fig. 2b). This suggests that the LRP component is involved to a lesser extent than the RP in encoding auditory consequences of self-generated actions. Bayesian analysis comparing the two LRPs yielded a Bayes factor of 0.85, thus providing weak support to the "null hypothesis" stating that there is no difference in LRP amplitude between motor + sound and motor-only conditions.

Finally, we performed a Bayesian factor analysis to directly compare the modulatory effects of active sound generation on RP and LRP. Using BIC, we found that the Bayes factor was 0.59, thus providing weak support to the "null hypothesis" stating that there is no difference between modulation of RP and LRP by self-generated sounds.
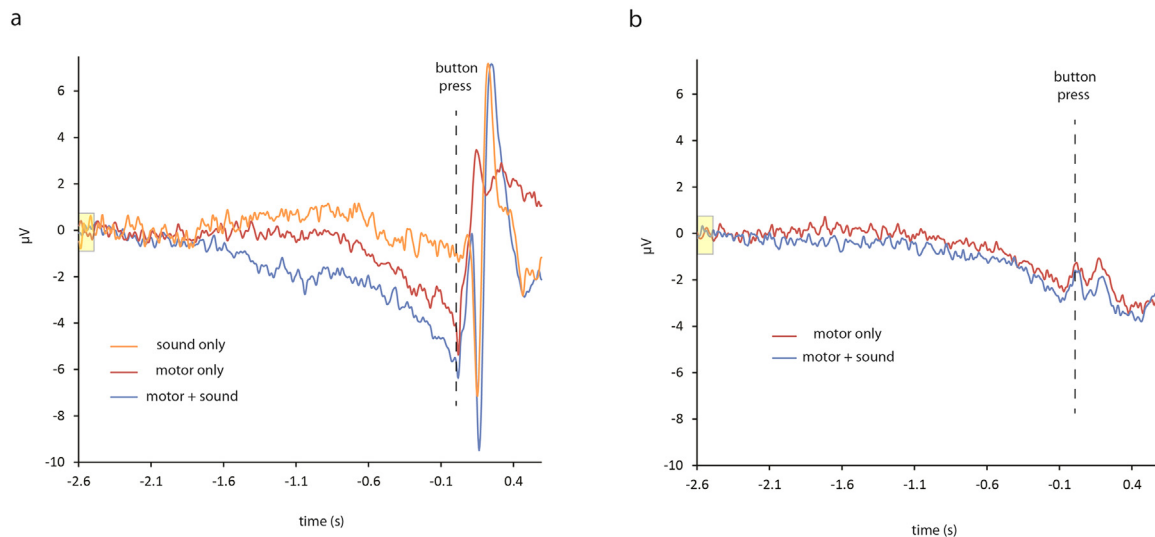
**Fig. 2.** Readiness Potentials. (a) Mean readiness potential across subjects (n = 12) was significantly more negative in the motor + sound condition (blue) compared with the motor-only condition (red). The signal preceding sound delivery in sound-only condition (orange) was not significantly different than zero. The marked yellow area denotes the time interval used as baseline. (b) Lateralized readiness potential time-courses. The mean LRP prior to button press in the motor + sound condition was not significantly more negative than the mean LRP preceding motor-only condition. The marked yellow area denotes the time interval used as baseline.

## 4. Discussion

In the current study, subjects performed voluntary, self-paced button presses that were either associated with auditory consequences or not. We found that readiness potential prior to sound-triggering button presses was characterized by stronger negativity compared with the readiness potential preceding button presses with no auditory consequences. Importantly, this difference could not be attributed merely to the expectation of an auditory event which is present in one motor act and not the other.

It has been suggested that sensory regions undergo top-down modulation by the motor system during voluntary action execution (Crapse and Sommer, 2008). Accumulating theoretical (Schurger et al., 2012; Wolpert et al., 1995) and empirical (Eliades and Wang, 2003; Haggard et al., 2002; Voss et al., 2006) evidence suggest that the modulatory effect of self-generated actions on neural activity and perception starts prior to execution of an action or actual delivery of the re-afferent stimuli. This is compatible with reports of attenuated sensation even during the preparatory period prior to movement (Voss et al., 2006).

In the current study, we show that expectation of self-generated action consequences starts to modulate neural activity prior to execution of the sound-triggering actions. This, could potentially activate and prepare the motor-sensory network for perception of self-generated stimuli prior to its actual delivery/generation (Ford et al., 2013; Vercillo et al., 2018). Accordingly, Jo et al. (2014) found an association between the early RP phase and behavioral reports of temporal perception of ensuing stimuli in the auditory domain. The authors report that subjects with more negative early RP showed greater intentional binding, namely, these subjects perceived self-generated sounds as being closer in time to the sound triggering actions. Together, these results suggest that the early RP component preceding sound-triggering actions is related to expected perception of self-generated auditory consequences.

In terms of functional neuroanatomy, readiness potential and lateralized readiness potential components are believed to reflect neural activity in different brain areas. While the cortical source of readiness potential is believed to reside in frontal, high-order areas of the motor system, such as SMA and pre-SMA (Lang et al., 1991; Shibasaki and Hallett, 2006; Yazawa et al., 2000), the lateralized readiness potential is believed to be related to more specific, low-level motor components

originating in M1 contralateral to the executing effector (Eimer, 1998; Haggard and Eimer, 1999). We found that sound triggering actions modulate RP, but not LRP amplitude, although our Bayesian analysis suggests that there is no substantial difference between RP and LRP modulation. This notion is compatible with reports showing encoding of sensory consequences for self-generated actions that occur not only in high-order motor areas, such as SMA and lateral pre-motor cortex (Christensen et al., 2007; Cui et al., 2014; Haggard and Whitford, 2004; Makoshi et al., 2011; Reznik et al., 2015b), but also in primary motor cortex (Eisenberg et al., 2011; Reznik et al., 2015b, 2014). Future research is needed to delineate the roles of low and high level motor regions in encoding sensory consequences of voluntary actions.

According to the ideomotor theory (Greenwald, 1970), self-generated motor actions represent internalized mental images of their predicted sensory consequences. Our results support this view by showing that motor-related preparatory brain activity is different between sound-triggering and silent button presses. Thus, our results support this theory by showing that RP does not only reflect motor planning, but also early coding of the internal sensory image. Moreover, the ideomotor theory suggests that voluntary actions should lead to modulated sensory representation of the evoked reafferent stimulus (Shin et al., 2010). This view is consistent with the current and previous physiological studies showing that perceived loudness of self-generated sounds is modulated compared with sounds perceived in a passive manner (Reznik et al., 2015a; Weiss et al., 2011).

Current findings have also implications for studies evaluating differences in EEG evoked responses to externally-generated and self-generated auditory stimuli (see Horváth, 2015 for a review). These studies typically use a short time window of 100–200 ms prior to sound onset as a baseline to calculate the amplitude of auditory evoked potentials. The underlying assumption is that the brain signals across conditions are similar during the baseline window. In the current study we show that this assumption does not hold and that differences in EEG signal between self and externally-generated auditory stimuli are evident in this time window. We suggest that for complete evaluation of forward model function, alongside with stimulus-evoked brain activity, one should also explicitly examine the brain activity preceding stimulus onset.

It is important to note that the motor-only condition was not completely devoid of sensory feedback. Although this condition did not involve auditory stimulation, it did involve proprioception and

somatosensory feedback due to finger movement and button press and visual feedback of the hand. Nonetheless, we assume that similar sensory feedback was present in the motor + sound condition.

There is an inherit difference in predictability of onset between self-generated and externally-generated sounds. Previous studies examining auditory evoked responses have introduced visual count-down to minimize differences in predictability between self-generated and externally-generated sounds. In these studies no effect of predictability was found on behavioral (sensory attenuation), and physiological (evoked response) measures (e.g., Mifsud et al., 2016; Weiss and Schütz-Bosbach, 2012). In the current study, we examined pre-stimulus activity rather than evoked responses and therefore could not use pre-stimulus prediction cues that would have confounded the RP signal. Instead, to increase predictability in the externally-generated sounds, we used a fixed stimulation rate. Nevertheless, it cannot be ruled out that differences in predictability between the two conditions still remain. Additionally, it can be argued that motor + sound and motor-only conditions differ in their attentional demands and that such differences might have contributed to the reported differences in RP. Previous studies addressing the issue of attention did not find significant differences in evoked responses or sensory attenuation effect (Saupe et al., 2013; Timm et al., 2013). Although in the current study we examined pre-stimulus activity rather than evoked responses, we believe that differences in attention are unlikely to explain our current results.

Regarding the neuroanatomical source of RP differences, EEG is limited in spatial resolution and distinguishing signals arising from motor and auditory cortices is particularly difficult. In the current study we assumed that the source of RP is in motor cortex. However, the modulation of RP amplitude we report could in principle result from changes in auditory activity prior to self-generated auditory stimuli (Eliades and Wang, 2003; see also Hughes and Waszak, 2014 for visual domain).

To conclude, we report that expectation of sensory consequences coupled to voluntary actions modulates the dynamics of preceding neural activity and suggest that motor areas are involved in encoding of such sensory expectations.

## Acknowledgements

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