Consequences matter: self-induced tones are used as feedback to optimize tone-eliciting actions

Bence Neszmélyi[1,2], János Horváth[1]

[1]Institute of Cognitive Neuroscience and Psychology, Research Centre for Natural Sciences, Hungarian Academy of Sciences, Budapest, Hungary

[2]Budapest University of Technology and Economics, Budapest, Hungary

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Address correspondence to:

Bence Neszmélyi
Institute of Cognitive Neuroscience and Psychology, RCNS, HAS
P.O.B. 286,
1519
Budapest,
HUNGARY
Phone: +36 1 382 6819
E-mail: neszmelyi.bence@ttk.mta.hu

Abstract

Experimental paradigms investigating the processing of self-induced stimuli are often based on the implicit assumption that motor processes are invariable regardless of their consequences: It is presumed that actions with different sets of predictable sensory consequences do not differ in their physical characteristics or in their brain signal reflections. The present experiment explored this presumption in the context of action-related auditory attenuation by comparing actions (pinches) with and without auditory consequences. The results show that motor processes are not invariable: Pinches eliciting a tone were softer than pinches without auditory effects. This indicates that self-induced auditory stimuli are not perceived as irrelevant side-effects: The tones are used as feedback to optimize the tone-eliciting actions. The comparison of event-related potentials (ERPs) related to actions with different physical parameters (strong and soft pinches) revealed a significant ERP-difference in the time-range of the action-related N1 attenuation (strong pinches resulted in more negative amplitudes), suggesting that a motor correction bias may contribute to this auditory ERP attenuation effect, which is usually attributed to action-related predictive processes.

Keywords: hearing, voluntary action, sensory attenuation, sensory feedback, motor control, ERP

Introduction

Interactions between sensory and motor systems are often investigated in paradigms which attempt to decompose processing changes into sensory- and motor-related effects. The interaction between the two systems can be examined from various perspectives. Some studies explore how movements are affected by sensory stimuli that are causes (Cisek & Kalaska, 2005; Eimer, Hommel & Prinz, 1995; Green & von Gierke, 1985) or goals (Hommel, 2009; Prinz, 1987) of the actions. Another line of research, however, is oblivious to stimulus-related variability in motor processes--considering motor processes invariable regardless of their sensory consequences--and instead focuses on how the processing of self-induced sensory events is influenced by the actions that elicit them. At first glance, this approach seems plausible: Actions precede their sensory consequences, so motor processes may influence the processing of subsequent sensory events, but it would appear unreasonable that the sensory consequence could affect the eliciting movement. In this context self-generated stimuli are simply interpreted as irrelevant side-effects of the actions. This reasoning, however, disregards two important aspects of action-stimulus relationships. First, actions are usually performed more than once, and although retrospective processes can not influence actions that precede them, they may effect similar actions that are performed subsequently. Focusing exclusively on the predictive aspect neglects the fact that the stimulus also contains information about the action: Even in the most simple action-effect relation, the stimulus informs the agent that the action was successful. If actions are repeated in a sequential manner, such retrospective information could play an important role in controlling the movements. As a consequence the presence or absence of reliable action feedback may affect how actions are planned and executed. Second, many theories (Hommel, 2009; Hommel, Müsseler, Aschersleben & Prinz, 2001; Prinz, 1990; van der Wel, Sebanz & Knoblich, 2013) would argue for an even stronger link between motor and sensory processes,

implying that neither one can be altered without also affecting the other. The theories based on the ideomotor principle (Greenwald, 1970; Hommel et al., 2001; Prinz, 1987) for example, regard self-generated stimuli not simply as consequences but also as goals of the actions. As the goals play an important role in the selection of appropriate motor commands, the addition or elimination of an action-effect may have considerable influence on the motor parameters as well.

Disregarding potential stimulus-to-action effects not only limits the scope of research, but it could also bias the estimation of sensory effects that are generally attributed to predictive processes. Research investigating the processing of self-induced sounds is a typical example of focusing exclusively on the perceptual aspect of motor-sensory interactions. Studies on this topic often compare behavioral responses or physiological signals related to stimuli which are physically identical, but are initiated by one's own actions, or by external agents; signal differences in such arrangements are attributed to action-related processing activities. When decomposing a physiological signal related to a compound action-stimulus event (e.g., a button press followed by a sound), the stimulus-related contribution to this signal is often estimated by subtracting a signal related to an action-only event (e.g., a button press not followed by a sound). The assumption underlying the subtraction logic is that the action--and its contribution to the physiological signal--is identical in these two types of events. Whereas this assumption is valid if compound action-stimulus events occur only by chance (e.g., Horváth, Maess, Baess, Tóth, 2012), it might be invalid if there is a contingent relationship between the actions and the stimuli. The goal of the present study was to test the validity of this assumption in the context of action-related auditory attenuation; that is, we investigated whether movement parameters differed when an action consistently elicited a sound, and when it did not.

Action-related sensory attenuation refers to the phenomenon that self-induced stimuli elicit lower intensity sensory percepts or physiological responses than those induced by external sources despite being physically identical (Bays, Wolpert & Flanagan 2005; Blakemore, Wolpert & Firth, 1998; Cardoso-Leite, Mamassian, Schütz-Bosbach & Waszak, 2010; Hughes & Waszak, 2011; Sato, 2008; Weiss, Herwig & Schütz-Bosbach, 2011). In the auditory domain a number of studies reported that sounds initiated by one's own actions elicit lower amplitude event-related potentials (ERPs) than those initiated by other agents (Baess, Jacobsen & Schröger, 2008; Baess, Horváth, Jacobsen & Schröger, 2011; Baess, Widmann, Roye, Schröger & Jacobsen., 2009; Horváth, 2013a, 2013b; Martikainen, Kaneko & Hari 2005; SanMiguel, Todd & Schröger, 2013; Schäfer & Marcus, 1973; Timm, SanMiguel, Saupe & Schröger, 2013; Timm, Schönwiesner, Schröger, & SanMiguel, 2016). Because the actions elicit ERPs overlapping the auditory ERPs, most studies estimate the auditory ERP-contribution to the action-sound ERP waveform by subtracting an action-related ERP elicited in a different condition in which the actions do not result in sound-elicitation. This *corrected* ERP waveform is then compared to the auditory ERP measured when the sequence of sounds is replayed without concurrent actions. If actions and action-related ERPs differed between conditions, this might be reflected in the corrected ERP waveform, that is, the estimate will be biased.

In the present experiment a conventional action-related auditory ERP attenuation paradigm was administered; however, participants were instructed to apply force-impulses on a force-sensitive resistor (FSR) instead of pressing a button. The FSR's resistance changes with the force applied to it, which made it possible to use it both as an input device and as an instrument to record physical parameters of the actions. By co-recording the FSR-signal with the EEG, the temporal characteristics of force application could be measured in the two conditions in which actions were required from participants: in the motor-auditory condition,

when the applied force exceeded a threshold, a tone was triggered, in the motor condition, force application did not result in a tone. The goal of the experiment was to compare physical action parameters in these two conditions to determine whether motor processes are indeed unaffected by changes in their sensory consequences.

Method

Participants

Twenty young adult volunteers recruited through a student part-time job agency participated in the experiment for monetary compensation. They gave written informed consent after the experimental procedures were explained to them. Data from four participants were not included in the analysis due to exceeding number of artifacts in the electroencephalogram (EEG) recordings, which resulted in the rejection of more than 50% of the ERP epochs from the analyses. The final sample consisted of sixteen participants (aged 19–27 years, $M = 22.8$ years, 6 women, all right handed). All reported normal hearing and no history of psychological or neurological disorders.

Stimuli and procedure

During the experiment participants were seated in an armchair in a sound-proofed room.

As the goal of the experiment was to study the effect of auditory stimuli on the actions that generate them, participants had to perform self-induced movements, which elicited a tone (motor-auditory condition), or did not result in auditory consequences (motor condition). To emphasize the intentional aspect of the actions, instead of asking them to execute evenly paced actions, participants were instructed to perform self-paced actions so that the interval between them is never shorter than 2 s or longer than 6 s. To keep the task challenging, they

were also asked to distribute actions during the blocks in a way that the histogram of the between-action intervals (displayed at the end of each block) would show a uniform distribution between 2 and 6 s. In most similar experiments the action is a button press. Most conventional response devices produce a well-identifiable sound (click) when the device is operated. The presence of such sounds could bias action-related sensory attenuation estimates in various ways (Horváth, 2014). For example, changes in the processing of the action-coupled, experimentally manipulated sensory consequences (sounds or visual stimuli elicited by the actions) could be simply caused by attention being oriented to the clicks, resulting in reduced attention and consequentially attenuated ERPs for the experimentally relevant action-coupled self-induced stimuli. To avoid such issues, it is recommended to use devices that do not produce transient sounds or even devices that require no mechanical interaction at all (e.g., a light-gate). To avoid the effect of clicks (while also making possible the recording of the physical parameters of the actions), in the present experiment participants were instructed to pinch an FSR (FSR 400, Interlink Electronics, Westlake Village, California, USA) mounted on a plastic sheet held between the index finger and the thumb. This paper-thin (0.3 mm) device changes its resistance (without substantially changing its form) when pressure is applied to it. In the present setup, when the resulting voltage change exceeded a preset threshold (1.25 V corresponding to a force-equivalent measure of 3.603 a.u.; the maximum voltage was 4.3 V, corresponding to 819.308 a.u.), the action was considered successful, and in the motor-auditory condition a sine tone was triggered. (In the motor condition the applied force and the timing of the actions were recorded, but actions did not elicit a tone.) The FSR produced no unintended action feedback: as pinches did not result in substantial movement, they did not produce audible sounds in themselves, and the success of the action was not signaled by a distinct external tactile event.

Sound levels in the experiment were adjusted individually, so the experiment started with determining the participants' 75% hearing threshold for 1000 Hz tones, using an adaptive procedure (Kaernbach, 1990). After that, to familiarize themselves with the device and the task, participants completed a three-step training phase. First, they were familiarized with the necessary force needed to produce a successful interaction with the device by freely interacting with a real-time visual display of the FSR-signal, in the form of a blue vertical bar which changed its height in proportion to the FSR-signal. When the FSR-signal was above the fixed action-threshold, the color of the bar changed to green. In order to keep the applied force within the measurement-range of the FSR, if a second, higher threshold (3.75 V, 307.939 a.u.) was exceeded, the bar color changed to red. Participants were made aware of these possibilities, and were instructed to explore the pinch-force needed to produce these color changes. Second, participants learned the time-interval production task with online visual feedback: a histogram of the between-action intervals was presented on the screen, and was updated after each action. In the motor practice block, pinching the FSR resulted in no sound; in the motor-auditory practice block, pinching the FSR resulted in a 1000 Hz sine tone (see below.) Third, participants were administered short versions (30 trials) of the motor and motor-auditory experimental blocks. In these practice blocks the histogram of the produced between-action intervals was only displayed at the end of the blocks.

After the training phase, the electrode cap was mounted, and the experiment started. The experiment comprised three conditions, the *motor-auditory*, the *motor*, and the *auditory* conditions. In the *motor-auditory condition*, participants had to perform the time-interval production task in the 2-6 s time-range. Pinching the FSR with sufficient force resulted in a 1000 Hz pure tone. The histogram of the between-action intervals was displayed at the end of the blocks. The timing of the tone sequence produced in the motor-auditory condition was recorded, and replayed in the *auditory condition*. In this condition participants simply listened

to the tones, without performing actions (the FSR was set aside; i.e., they did not hold the FSR in the auditory condition). To address the differences in motor activity between motor-auditory and auditory conditions, a *motor condition* was also included. In this condition, participants were instructed to perform the same time-interval distribution production task as in the motor-auditory condition, but pinching the FSR did not result in a tone.

The experiment consisted of 15 blocks (five blocks for each condition), with 60 (tone, action, or action-tone) events per block. The conditions were presented in block-triplets. The triplets always started with a motor-auditory block, which was followed first by a motor and then an auditory block for half of the participants, while the other half performed the remaining two blocks in reverse order (auditory first then motor). The blocks were separated by short breaks, with a longer break at around the middle of the session as needed. In this design, motor-auditory blocks always preceded the motor and auditory blocks, which may bring sequence effects about. To prevent this, for every participant one block from each condition was set aside. These blocks were chosen systematically to ensure a balanced block order across participants for the remaining blocks: Participants were divided into three groups of equal size. Omitted from analysis were the first (motor-auditory) block and the last two (auditory and motor) blocks of the experiment for the first group, the first two blocks and the last block for the second group, and the first three blocks for the third group. The blocks set aside were used to inform the choice of the electrode and time-windows for the statistical tests to be applied to the rest of the dataset (i.e., these blocks were excluded from subsequent analyses).

The 1000 Hz pure tones (100 ms long, including 5-5 ms linear rise and fall ramps) in the motor-auditory and auditory conditions were delivered through headphones (HD-600, Sennheiser, Wedemark, Germany), with a tone intensity individually adjusted to 40 dB above the 75% hearing threshold level. Due to hardware limitations, there was a 10 ms delay

between the moment when the pinch-threshold was exceeded and the sound onset. In all three conditions, continuous band-reject-filtered white noise was presented (Kaiser windowed finite impulse response--FIR--with cut-off frequencies of 600 and 1400 Hz, transition width of 3 Hz and stop band attenuation of 100 dB) in the headphones. The noise was used with the intention to enable the separation of the supratemporal and modality-non-specific N1 subcomponents (see Supplementary Material). The signal energy of the noise was 8 dB higher than that of the tones. The 800 Hz reject-bandwidth is much wider than the equivalent rectangular bandwidth of the auditory filter at 1000 Hz (which is about 133 Hz, Glasberg & Moore, 1990), that is, the tone was clearly audible despite the presence of the noise.

EEG pre-processing

The EEG- and FSR-signals were recorded by a Synamp2 amplifier (Compumedics Neuroscan, Victoria, Australia), with a sampling rate of 1000 Hz (online low-pass filter at 200 Hz). The EEG was recorded from 61 Ag/AgCl electrodes mounted on an elastic cap according to the 10% system (Nuwer et al., 1998). The reference electrode was positioned on the tip of the nose, the ground electrode on the forehead. Additional electrodes were placed at the mastoids. Horizontal electrooculogram (EOG) was recorded by electrodes at the outer canthi of the two eyes in a bipolar setup, while the vertical electrooculogram was calculated offline as the difference between the signal recorded at Fp1 and the electrode placed under the left eye.

The EEG was filtered offline using a 30 Hz lowpass-filter (Kaiser-windowed FIR, beta: 5.52, 1771 coefficients, stop-band attenuation: min. 50 dB, transition bandwidth: 2 Hz). 550 ms long epochs corresponding to actions, action-tone events and tones were extracted, including a 150 ms pre-event period. The epochs were time-locked to the time-point when the FSR-signal exceeded the threshold. (In the auditory condition, in which no actual actions

occurred, the timing of the actions previously recorded in the corresponding motor-auditory condition served as reference points.) The first and last trial of each block and epochs with voltages exceeding 100 µV at any channel were excluded from analysis. Occasionally, small fluctuations in the FSR-signal caused the registration of two actions in rapid succession, as the FSR-signal dropped below and then exceeded the threshold. As only those events were included in the analysis which followed the previous event within a 2-6 s interval (as defined by the interval-production task), epochs related to such double-actions were automatically discarded. The remaining epochs were averaged for each condition and participant, relative to a 150 ms pre-event baseline.

For examining the readiness potentials (RPs) and lateralized readiness potentials (LRPs), 800 ms long epochs (with 600 ms pre-event and 200 ms post-event periods) were extracted. The epochs were time-locked to the moment when the FSR-signal exceeded the threshold. Only epochs corresponding to actions separated by at least 3 s from the preceding action were included. Epochs corresponding to the first and last trial of each block, and epochs with signal-ranges exceeding 100 µV at any channel were excluded from the RP- and LRP-analyses.

ERP analysis – N1 and P2 attenuation

As described above, some of the experimental blocks (first or last auditory block for each participant) were used only to inform the electrode and time-window choices for the ERP amplitude comparisons, but these were not included in the analyses themselves. N1- and P2-peak latencies and the electrodes of the maximal signal peak were identified in group-average tone-related ERPs elicited in these auditory blocks. Individual N1 and P2 amplitudes were calculated in the remaining blocks as signal averages in 20 ms windows centered at these time-points, at these electrodes. To estimate the auditory ERP contribution to the motor-

auditory ERP, the motor ERP was subtracted from the motor-auditory ERP. The amplitude of this *corrected motor-auditory* waveform in the N1 and P2 time intervals was compared to those of the auditory waveform with two-tailed paired Student's t-tests.

The topographical distribution of the ERP attenuation effect was compared to that of the underlying ERP waveform by a Signal (auditory ERP vs. ERP attenuation-effect) × Electrode (Fz, Cz, Pz, Oz) ANOVA with the amplitudes vector-normalized using the method described by McCarthy and Wood (1985). A significant interaction in this analysis would mean that the effect was not a modulation of the underlying ERP, but reflected (at least in part) the superposition of an ERP of different origin. Generalized eta-squared effect sizes (Bakeman, 2005; Olejnik & Algina, 2003) are reported.

A secondary goal of our experiment was to investigate the contribution of auditory and modality-non-specific processes to the N1 attenuation effect, thus various N1 subcomponents were also assessed separately. For the analysis regarding the supratemporal and modality-non-specific N1 subcomponents see Supplementary material.

Pinch-force analysis

FSR-signal values (voltages) were transformed into force values according to the logarithmic function depicted in the FSR 400 Series Data Sheet (Interlink Electronics, 2016; because the device was not calibrated, we use arbitrary units--a.u.--instead of Newtons as measurement unit). Each action was characterized by the peak amplitude (maximum) of the force signal in the 750 ms post-event period, and the latency of this maximum. Each participant was characterized by the average of the peak forces and -latencies measured in the motor-auditory and motor conditions. The average peak forces and latencies in the motor and motor-auditory conditions, as well as between-action intervals were compared by paired Student's t-tests.

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To visualize potential temporal changes in the action parameters, over the course of the experiment, for each trial, in each block the individual FSR peak values were averaged across participants, and plotted. Visual inspection of these plots suggested that the applied force changed systematically within the blocks. To statistically explore these tendencies and their relation to the sensory feedback following the actions, for each participant and condition FSR peak amplitudes measured respectively in the first, second, third, and fourth quarter of the blocks were averaged. These average FSR peak amplitudes were then submitted to a Condition (motor, motor-auditory) × Position (1st , 2nd, 3rd and 4th block-quarter) ANOVA.

Because participants applied significantly stronger pinches in the motor-, than in the motor-auditory condition, it could be hypothesized that pinch-force differences contributed to the measured ERP attenuations. To test this possibility, ERPs were averaged separately for actions with softer- and stronger-than-median pinches for each participant in both motor and motor-auditory conditions. Average ERP signals in 20 ms time-windows centered at the maxima of the N1 and P2 attenuation effects (i.e., the time-points and electrodes of the largest N1 and P2-differences between ERPs in the auditory and motor-auditory conditions) were compared between strong and soft FSR-pinches by Student's t-tests separately in the motor and motor-auditory conditions.

Readiness potential and lateralized readiness potential

As described above, the discarded motor and motor-auditory blocks (which were excluded from further statistical tests) were used to identify the relevant electrode for the analyses conducted with RPs and LRPs. Using the group-average RP from these blocks, the electrode with the largest peak in the 200 ms time-range preceding the action was selected. RP amplitude was characterized by the average signal in the 100 ms preceding the pinches, relative to a -600 to -500 ms baseline. Lateralized readiness potentials (LRPs) were calculated

by subtracting the RP values at the right-hemisphere electrodes from the RPs at the corresponding left-hemisphere electrodes.

RPs and LRPs in the motor and motor-auditory condition were compared by Student's paired t-tests at the electrode with the highest RP amplitude in the discarded motor and motor-auditory blocks (see above). Pinch-force related effects were investigated by comparing RPs related to strong and soft (FSR peak amplitudes above and below median, respectively) pinches separately in the motor and motor-auditory conditions, using Student's paired t-test.

Results

Behavioral data

Participants complied with the instruction, and produced a close-to-uniform distribution of between-action intervals in the 2-6 s range (Figure 1). However, the mean between-action interval in the motor condition ($M = 4.007$ s, $SD = 0.275$ s) was significantly longer ($t(15) = -3.438$, $p = .004$) than in the motor-auditory condition ($M = 3.834$ s, $SD = 0.256$ s). (For this comparison only double-actions--as described previously--were excluded from the analysis. For all other statistics, however, all actions outside the 2-6 s time-range were disregarded).

N1 and P2 attenuation effect

Figure 2 shows N1-P2 waveforms elicited in the motor-auditory (both uncorrected and motor corrected) and the auditory condition. In the auditory condition the highest negative peak in the N1 (the 50-150 ms post-event) interval was at FCz with a latency of 117 ms (calculated from the blocks set aside). The analysis in this time-window and at this electrode showed a clear N1 attenuation: the N1 amplitude in the corrected motor-auditory waveform was significantly reduced in comparison to the auditory condition ($t(15) = -5.566$, $p < .001$).

A positive waveform following the N1 (referred to as P2 in the following, but see Discussion) could be identified in the auditory condition peaking at 236 ms after tone onset, at FCz (calculated from the blocks set aside). This waveform was also attenuated: the amplitude in the 226-246 ms interval in the corrected motor-auditory condition was significantly lower than in the auditory condition ($t(15) = 3.847$, $p = .002$).

The Signal (auditory ERP vs. ERP attenuation effect) × Electrode (Fz, Cz, Pz, Oz) ANOVAs of the vector-normalized amplitudes showed no interactions for N1 or P2. For the P2, the visual inspection of the topographies (Figure 3) revealed a difference: whereas in the auditory condition there were two temporal peaks at both sides of the central positivity, the ERP effect was characterized by a single central maximum. The two-way Signal × Electrode (T7, C3, Cz, C4, T8) ANOVA of the vector-normalized amplitudes exploring this difference showed a significant Signal × Electrode interaction ($F(1,15) = 6.871$, $p < .001$, $\eta^2 = .030$), that is, the topographies differed in the P2 time-range. This suggests that different sources contribute to the P2 waveform in the motor-auditory and motor conditions (Figure 3).

For analyses regarding the supratemporal and modality-non-specific N1 subcomponents see Supplementary material.

Pinch-force analyses

The FSR-signal showed a reversed U-shaped curve with a single peak for most actions (Figure 4). Participants applied more pressure when the pinch did not result in a tone: The mean peak force was significantly higher ($t(15) = 5.081$, $p < .001$) in the motor (amplitude: $M = 239.276$ a.u., $SD = 198.041$ a.u.) than in the motor-auditory (amplitude: $M = 51.004$ a.u., $SD = 76.642$ a.u.) condition, and the peak was also reached later ($t(15) = 8.628$, $p < .001$) in the motor (latency: $M = 133$ ms, $SD = 4$ ms) than in the motor-auditory (latency: $M = 77$ ms, $SD = 2$ ms) condition.

The peak amplitude of the FSR-signal appeared to change from action to action during the blocks in a systematic manner (Figure 5). In the motor-auditory condition, the amplitudes decreased as a function of time indicating that participants applied less and less force during the course of each block. In the motor condition, the opposite tendency could be observed: within each block, the peak amplitude seemed to increase. To explore whether these observations were statistically supported at least in a post hoc sense, a Block position (1st, 2nd, 3rd, 4th quarter) × Condition (motor, motor-auditory) ANOVA of the individual mean FSR-peak amplitudes was calculated. The ANOVA revealed a significant condition main effect: ($F(1,15) = 26.180$, $p < .001$, $\eta^2 = .615$) and a significant Block position × Condition interaction ($F(1,15) = 17.847$, $p < .001$, $\eta^2 = .047$). To follow-up on this result, one-way block position ANOVAs were conducted separately, which indicated an effect of block position in both motor ($F(1,15) = 10.884$, $p = .005$ $\eta^2 = .420$) and motor-auditory conditions ($F(1,15) = 6.698$, $p = .021$, $\eta^2 = .309$). In the motor-auditory condition, pairwise t-tests revealed a significant difference between the first block quarter and all other block quarters and between the second and fourth block quarters, indicating that during the course of the blocks pinch-force decreased compared to the initial values (1st - vs. 2nd: $p = .032$, 1st vs. 3rd: $p = .025$, 1st vs. 4th: $p = .021$, 2nd vs. 3rd: $p = .133$, 2nd vs. 4th: $p = .033$, 3rd vs. 4th: $p = .074$). In the motor condition force values were larger in the later block quarters, and all comparisons between block quarters were significant (1st - vs. 2nd: $p = .036$, 1st vs. 3rd: $p = .013$, 1st vs. 4th: $p = .005$, 2nd vs. 3rd: $p = .030$, 2nd vs. 4th: $p = .005$, 3rd vs. 4th: $p = .027$).

Pinch-force and within-block-position related ERPs

The pinch-force differences between the motor and motor-auditory condition may be reflected in the action-related cortical potentials, which may also contribute to the observed ERP difference between the auditory and motor-auditory conditions. That is, the differences between the actions may be also reflected in the action-related ERPs. Because the auditory

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contribution to the motor-auditory ERP is estimated by subtracting the motor ERP, this may bias the calculations.

One way to compensate for the potential bias would be to select matching epochs from the motor-auditory and motor trials with similar peak forces, and calculate average ERPs from the force-matched subsets of epochs. (A more conservative matching approach would be to select motor-auditory epochs in which the applied force would exceed that of the matched motor trial in each case.) Unfortunately, such an analysis could not be performed, as peak force ranges overlapped only slightly between conditions, and the number of epoch-pairs that could have been force-matched was very low.

To test for the existence of the hypothetical bias, that is, whether pinch force differences contributed to the attenuation effects, ERPs related to stronger- and softer-than-median pinches were compared (using Student's t-tests) in the motor and the motor-auditory conditions, in the time-windows centered at the maxima of the N1 and P2 attenuation effects (i.e., the largest difference between the auditory and corrected motor-auditory ERPs, which peaked at 138 ms and 239 ms at FCz, and Cz respectively). A significant difference was only found in the time-range of the N1 attenuation effect in the motor condition ($t(15) = 3.297$, $p = .005$; Figure 6), showing that strong pinches resulted in more negative ERP amplitudes. The topography of the motor condition strong-minus-soft ERP difference in this time-range showed a frontocentral negative maximum (Figure 6, bottom). Because pinch force was generally stronger in the motor than in the motor-auditory condition, this result supports the notion that the motor-auditory-minus-motor difference waveform receives a force-difference-related ERP contribution, which enhances the N1 attenuation effect.

As the lack of significant force-related effect in the motor-auditory condition could be caused by the smaller force differences between strong and soft pinches in this condition, this

difference was calculated for each participant and condition (subtracting the mean FSR-force maximum of the soft pinches from the mean maximum of the strong pinches). A Student's paired t-test indicated that the difference between strong and soft pinches was significantly larger ($t(15) = 5.737$, $p < .001$) in the motor ($M = 128.900$ a.u., $SD = 55.569$ a.u.) than in the motor-auditory condition ($M = 45.248$ a.u., $SD = 46.173$ a.u.).

RP and LRP

The RP peaked at C3 (in the motor and motor-auditory blocks set aside), and RP amplitudes measured at this electrode (Figure 7) were significantly higher ($t(15) = -2.266$, $p = .039$) in the motor than in the motor-auditory condition. No significant RP amplitude differences were found between RPs related to stronger- and softer-than-median pinches (Figure 7) in the motor or the motor-auditory condition (two-tailed, paired Student's t-tests).

RPs in both conditions were lateralized, with larger amplitudes on the left side (contralateral to the action). However, no difference was found in the LRPs between motor and motor-auditory conditions.

<center>**Discussion**</center>

Studies investigating action-related auditory ERP attenuation generally assume that actions are invariant irrespective of their action-effects (Horváth, 2015). While reproducing the well-known N1 and P2 attenuation effects, the present experiment revealed action-effect-related differences in movement parameters, which is not consistent with this assumption. The results show that participants' pinches were softer when pinches consistently elicited an auditory action-effect (in the motor-auditory condition) in comparison to the condition in which an auditory action-effect was absent (motor condition). Moreover, differences in pinch-force also influenced the ERP in the time-range of the action-related N1 attenuation effect: the

ERP was more negative for stronger pinches in the motor condition, which demonstrates that a motor correction bias might contribute to the N1 attenuation effect.

Action-related ERP attenuation

The experiment replicated previous findings on action-related auditory N1 attenuation: The N1 waveform elicited by self-induced tones was clearly reduced compared to those elicited by externally generated sounds. (For a more elaborate discussion of the N1 attenuation effect and the role of auditory and modality-non-specific factors see Supplementary material.) Reduced amplitudes could also be observed for the subsequent positive component. Action-related P2 attenuation was reported in a few recent studies (e.g., Horváth et al, 2012; Knolle, Schröger, Baess & Kotz, 2012; San Miguel et al., 2013), the latency of the positive waveform in the auditory condition of the present study (236 ms after stimulus onset), however, makes the interpretation of this waveform ambiguous: It could be interpreted as P2, or as a P3a, especially because an earlier positivity could be observed in the motor-auditory waveform. That the positive waveform might receive contributions from multiple sources is also indicated by the presence of local temporal maxima observed beside the frontocentral maximum in its topography. Similar waveforms could be observed in a few previous studies (Baess et al., 2011; Knolle et al., 2012--interpreted as P3a or P2, respectively). Since P3a probably reflects involuntary attentional processes triggered by unpredictably occurring sounds (Friedman, Cycowicz & Gaeta, 2001), this could indicate that the tones presented in the auditory condition with an irregular SOA elicited this component with higher amplitude than the predictable, self-induced sounds did.

Pinch-force

The finding that differences in the sensory consequences of the actions were reflected in the physical action parameters was robust: the difference between actions with and without

elicited tones was clearly evident in the pinch-force profiles (the maximum of the FSR-signal) of each participant. Interpreting these between-condition force-differences seems straightforward. We hypothesize that they reflect a difference in the action-goals in the motor and motor-auditory conditions. In the experimental setup the primary objective during task performance--irrespective of action-effects--is to successfully interact with the device. Whereas one may achieve this goal simply by exerting maximal force on each occasion irrespective of the presence or absence of an auditory consequence, we hypothesize that the presence of the auditory action-effect provides an opportunity to optimize the applied force. Assuming that one objective is to minimize the exerted force, there are at least two plausible (although somewhat related) optimization goals. One is to reduce the uncertainty regarding the success of the interaction attempt: By utilizing the auditory consequence as feedback, participants could lower the applied force in the motor-auditory condition to a level that was sufficient for a successful interaction with the device. In the motor condition, however, only the less "useful" tactile feedback was available. That is, in the motor condition participants "overperform" to reduce the uncertainty concerning the success of the interaction attempt. A second alternative is that repeatedly performing an action may require less (cognitive) resources if the action has well-identifiable sensory consequences (Dyer, Stapleton, & Rodger, 2015). If a feedback modality (in this case the auditory stimulus) is removed, sensory stimulation from the remaining modalities (in this case tactile) has to be increased to provide a well-identifiable sensory consequence. Because more force results in more intense tactile feedback, this explanation also fits the results. Note that because the force-impulses were brief (ballistic), force optimization could occur only from trial-to-trial, and not during the course of each force exertion. The different force development trajectories within motor-auditory and motor blocks suggests that tuning the level of force in the motor-auditory blocks occurs mainly during the first 5-15 trials.

In most previous studies using typical action related ERP attenuation paradigms, which administer stimulation protocols with contingent action-effect relationships, the role of the self-induced sounds from the participants' point of view (what participants "do" with the sounds) remained unclear. The experimental logic (subtracting the motor ERP from the motor-auditory ERP) implies (tacitly) that a self-induced sound is an irrelevant side-effect that participants could simply ignore. The interpretation of the between-condition force-differences suggested above, however, implies that participants do not ignore, but actually rely on the auditory action-effect to adjust the actions and to maintain a successful interaction with the device.

Ideomotor theories of action control (Hommel, 2009; Shin, Proctor & Capaldi, 2010) suggest that sensory effects of the actions play a central role in the planning, control and adjustment of movements. These theories are supported by studies, which show that the learning and execution of movement sequences (Conde, Altenmüller, Villringer & Ragert, 2012; Stocker, Sebald & Hoffmann, 2003) and complex movements, like a golf swing, or playing a musical instrument (Dyer et al., 2015), can be enhanced by auditory feedback. The current study extends these results and indicates that even simple actions - like pinching a plastic sheet – can be affected by the sensory consequences of the movements.

Our experiment focused on paradigms in which participants elicited tones manually. The study of self-induced auditory stimuli, however, is not limited to sounds elicited by button-presses or finger-taps. A related line of research investigates how motor-based predictions affect the processing of speech (Curio, Neuloh, Numminen, Jousmäki & Hari, 2000; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Ventura, Nagarajan & Houde, 2009). In contrast to paradigms relying on manual actions, studies on self-produced speech have already suggested that self-induced speech sounds are used as feedback to adjust motor-processes, for example, to control the loudness of the produced sounds (Bauer, Mittal, Larson

& Hain, 2006; Heinks-Maldonado & Houde, 2005; Lane & Tranel, 1971). A reason for previous research neglecting this feedback aspect in paradigms using manual actions could be that the relation between action and sensory effect is less "organic" than in the case of self-produced speech. Movement parameters--like force--are only relevant in relation to the arbitrarily determined threshold for sound-triggering, and beyond this, action parameters do not influence the acoustic features of the elicited stimulus. For self-produced speech, however, properties of the sounds (e.g. loudness, duration) are directly related to the movement of the effector, which may well enhance their feedback function. It seems likely that similar enhancements could be present for all sound-inducing actions for which there is a strong coupling between movement and sound parameters. The present results show that even in the case of a simple threshold-based action-effect coupling, the feedback aspect cannot be neglected.

Motor correction bias

The idea that action-goals differ depending on the available sources of feedback would suggest that processes related to planning and control of movements are affected by the sensory consequences of the actions. Such differences should be also reflected in cortical activity both before and after the execution of the movements. Previous studies reported differences in the RPs in the movement planning phase that could be related to the expected consequence of the actions (Ford, Roach, Faustmann, Mathalon, 2007, 2008). RPs recorded in the current experiment also differed in the motor and motor-auditory conditions.

Whereas ERP-differences preceding action-effects can be unequivocally attributed to motor- or expectation-related processes, separating later ERP-differences related to motor- or sensory processing changes is not possible in most experiments, including the present one. To sidestep this issue, we examined whether force differences within the same condition could

result in ERP-differences in the time-ranges and at the recording sites of the N1 and P2 attenuations. Movement-parameter (e.g., force or velocity) differences may be reflected in the cortical potentials related to motor processes (Becker & Kristeva, 1980; Kristeva, Cheyne, Lang, Lindinger & Deecke, 1990; Kutas & Donchin, 1974; Oda, Shibata & Moritani, 1996; Siemionow, Yue, Ranganathan, Liu, & Sahgal, 2000; Slobunov, Hallett & Newell, 2004; Slobounov, Johnston, Chiang & Ray, 2002). Although the majority of the research focused on differences in the readiness potentials preceding action execution, studies show that the physical parameters can also have an effect on the motor-related ERPs that appear after the start of the actual movement (Becker & Kristeva, 1980; Slobunov et al., 2002; Slobunov et al., 2004; Wilke & Lansing, 1973). If such effects overlap the time-range of the auditory ERP components, then movement-parameter differences between actions with and without auditory consequences may contribute to, or even be the sole cause of the ERP-difference described as action-related ERP attenuation.

In the motor condition, stronger pinches elicited a more negative ERP than soft pinches in the time-range of the N1 attenuation effect, which suggests that the force-difference between the motor and motor-auditory condition can be manifested in the reduction of the corrected motor-auditory ERPs, which is usually interpreted as a self-generation effect. The topographical distribution of this strong-minus-soft difference in the motor condition is similar to the distribution of the N1 attenuation effect, which confirms the possibility of a force-related motor-correction bias. It is important to note that the force-dependent ERP-difference was not consistently observable in the present experiment: in the motor-auditory condition no such effect was found. The lack of a significant effect in the strong vs. soft comparison in the motor-auditory condition might have been caused by the relatively small force differences: the mean force difference between soft and strong pinches was nearly three times larger in the motor, than in the motor-auditory condition. The average force difference

between pinches in the motor and motor-auditory condition was, however, even larger than the average difference between strong and soft pinches in the motor condition. Thus it could be argued that the motor correction bias might be even larger than indicated by the force-related ERP-difference in the motor condition.

Although these results suggest that a force-related ERP-difference could in itself be sufficient to bring an "attenuation effect", that is, a motor-correction bias about, we assume that the between-condition action difference goes beyond the single parameter of applied force: the difference in physical parameters could reflect a fundamental, qualitative difference: the difference of action-goals in the two conditions (as discussed above). Due to the minimal overlap between the applied forces in the two conditions, we could not control for force-differences in the present study, and therefore, cannot provide strong evidence for this action-goal difference hypothesis. Our results nonetheless show that motor-control processes vary as a function of the feedback provided by the sensory consequences of the actions. This demonstrates that the concept of the motor-correction method itself needs to be closely examined in future studies, and if physical attributes of the actions indeed signal a difference in action-goals, the issue would not be solved simply by controlling the force-parameter.

Readiness Potentials

It has been previously suggested (Ford et al. 2007, 2008) that actions are preceded by neural activity reflecting the instantiation of the efference copy produced by the motor system, which is sent to sensory areas to predict the sensory consequences of the action. Consistent with this idea, Ford, Palzes, Roach and Mathalon (2014) have found that in healthy participants the amplitude of the lateralized readiness potentials (recorded before self-induced sounds) correlated with the magnitude of the action-related ERP attenuation, and that the

amplitude of RPs was higher in the motor-auditory than in the motor condition. In the present experiment, however, the opposite was observed: RPs were significantly larger in the motor than in the motor-auditory condition. This result is more in line with the studies showing that the amplitude of motor-related potentials correlates with the force of the following movement (Becker & Kristeva, 1980; Kristeva et al, 1990; Kutas & Donchin, 1974; Siemionow et al., 2000). The lack of force-dependent differences in RPs for softer-, and stronger-than-median pinches could again be explained by the within-condition differences being considerably smaller than those between the motor and motor-auditory conditions.

Device specificity

The ERP attenuation effects observed in the present experiment are very similar to those reported in other studies about this phenomenon, which suggests that our setup probably captures the relevant aspects of these previous studies. At this point, however, it cannot be assessed whether the observed motor parameter differences are specific to the response device, that is, whether substantial differences are also present when more conventional interaction devices (i.e., buttons) are used.

It is important to acknowledge that certain response devices may limit the motor parameter ranges leading to successful interactions, that is, some devices may not allow much freedom for action optimization. In the present setup, for example, selecting an FSR-signal threshold close to the maximum achievable pinch force level would eliminate the physical possibility for optimization, because the range of action-options would be too narrow. With the threshold setting used in the present study, action optimization was possible because many types of actions led to successful interactions. Due to usability issues, this is also true for most conventional devices, which are designed so that the parameter ranges of actions leading to successful interactions are wide. Whether participants are compelled to optimize their actions

if they get the chance, is a further question. For example, if the gains of choosing close-to-optimal actions is negligible, then no optimization will occur. In the present setup, it can be speculated that the relatively low force-threshold allowed a meaningful reduction of muscle effort, which compelled participants to optimize their actions.

The main difference between the FSR-based device and conventionally used (button-type) devices seems to be that applying a force impulse on the FSR does not result in substantial mechanical displacement or shape-change of the device, whereas pressing a button usually does. Because of this, no transient sound is generated by the FSR, in contrast to buttons, which often produce a transient sound (e.g., click, see Horváth, 2014). Furthermore, the moment of successful interaction with the FSR, that is, the moment when the force-threshold is exceeded, is not marked by a mechanical transient. Successful interaction with a button, however, is often signaled by a well-defined tactile event, for example, the start of the displacement, or reaching the end position after displacement. One may speculate that the absence of such marked tactile feedback in an FSR-based setup makes external feedback relatively more "valuable" than in a conventional response-device based setup. The idea that action-effects are differentially weighted during action planning has been also suggested by Memelink & Hommel (2012) in the context of the ideomotor principle. In the present context, a relatively highly weighted external auditory feedback may have amplified feedback-related differences in the present setup. With conventional response devices, the tactile feedback constantly available in both motor and motor-auditory conditions might allow one to apply forces closer to the optimum, that is, for such devices, the lack of an external auditory consequence could lead to a smaller force-difference between the conditions.

Although this may be the case, it is important to emphasize that humans have considerable freedom in the selection of task-relevant action effects for action representation (see e.g., Hommel, 1993). It is an interesting question, whether the availability of a constant

device-based feedback would compel participants to select the action-effects related to the operation of the device as primary action effects. One may intuitively argue that due to our everyday exposure to button-press based interaction devices (see Horváth, 2013a), in the motor-auditory condition most participants would regard the external sound as the primary, task-relevant action-effect. The plausibility of this argument is well illustrated by cases in which the otherwise redundant feedback becomes mixed. That is, when most actions consistently lead to the elicitation of both types of feedback (i.e., external sound and device-based feedback), an action eliciting an external sound without the accompanying device-based click would probably still be regarded as a successful interaction, whereas the absence of the external sound would be regarded as a failure despite the presence of the device-based click.

Obviously, further experiments are needed to clarify the influence of device characteristics on action-effect interactions. In light of the arguments above, however, it seems unlikely that the presently reported phenomena would be contingent on the response device used.

Summary

Many studies about action-related ERP attenuation assume that actions are invariable regardless of differences in their sensory consequences. The present study presents strong evidence against this assumption: Actions with and without contingent auditory consequences were physically different. Moreover, the results suggest that the physical differences are also reflected in the action-related ERPs, which may inflate the estimates of action-related auditory ERP attenuation.

The analysis of the action force-profiles and their development during the course of the experiment suggests that auditory effects were an important part of the goal structure associated with the experimental task, and not just a side-effect of the actions: Participants

used the auditory stimuli to optimize the tone-eliciting actions. These results support the idea that sensory effects are an integral part of the action representations, and play a fundamental role in the motor selection and action control processes.

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Author note

Bence Neszmélyi, Institute of Cognitive Neuroscience and Psychology, Research Centre for Natural Sciences, Hungarian Academy of Sciences; Department of Cognitive Science, Budapest University of Technology and Economics; János Horváth, Institute of Cognitive Neuroscience and Psychology, Research Centre for Natural Sciences, Hungarian Academy of Sciences.

Correspondence concerning this article should be addressed to Bence Neszmélyi, Institute of Cognitive Neuroscience and Psychology, Research Centre for Natural Sciences, Hungarian Academy of Sciences, P.O.B. 286, Budapest 1519, Hungary. E-mail: neszmelyi.bence@ttk.mta.hu
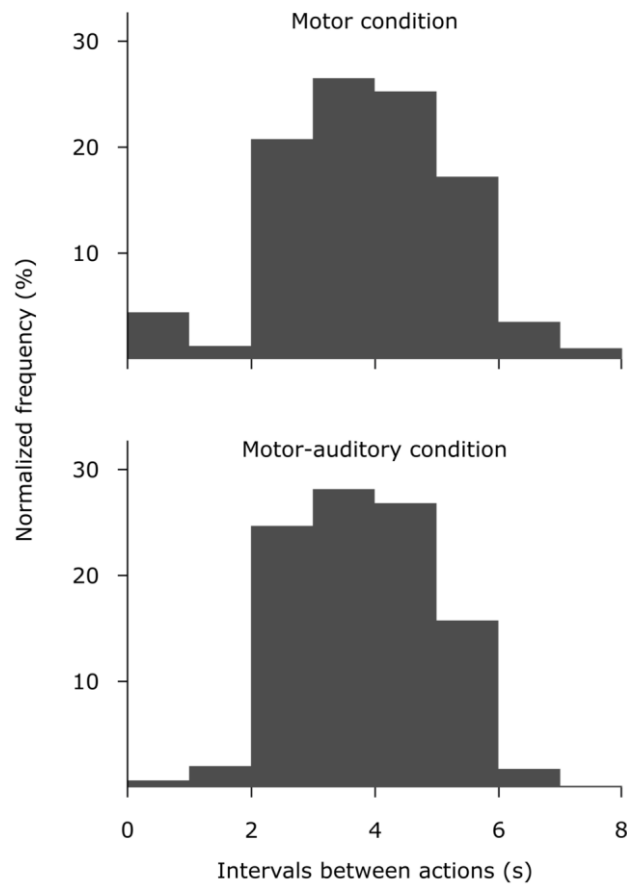
Figure 1. Histograms of time-intervals between pinches in the motor and motor-auditory

conditions. (Summary data of the 16 participants included in the analysis: all pinches of each

participant). Note that although all registered between-action intervals are presented

(including those which may have been erroneously registered as separate actions during the

release of a pinch, see Methods) only actions separated by at least 2 s from preceding actions

were included in the analyses.
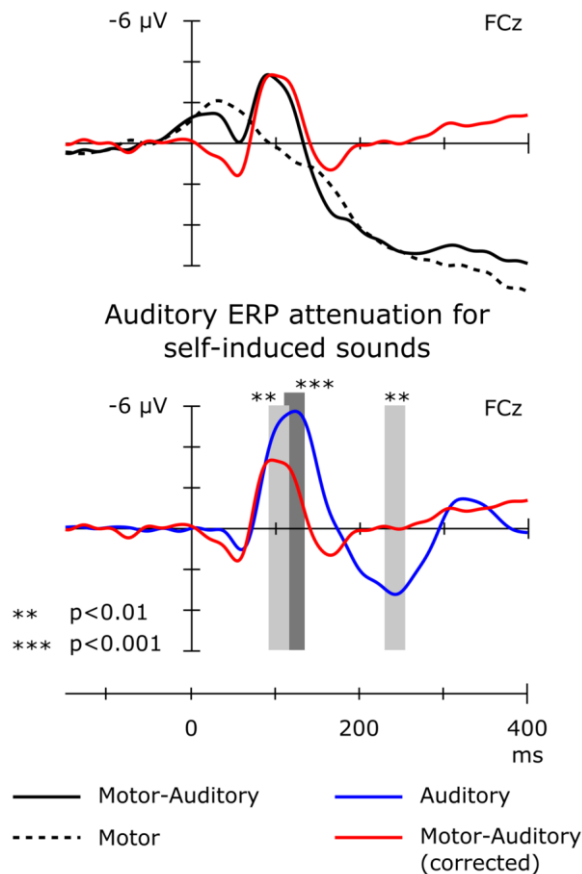
Figure 2. Group-average ERP waveforms elicited in the auditory, motor, and motor-auditory conditions. The figure on the top shows the estimation of the auditory contribution to the ERPs elicited by compound action-sound events. The corrected motor-auditory waveform was calculated by subtracting the ERPs elicited in the motor condition from the ERPs elicited in the motor-auditory condition. The figure on the bottom displays the group-average auditory and corrected motor-auditory waveforms. Grey bars mark the 20 ms time-windows used for amplitude measurements. P-values show significance levels of two-tailed, paired Student's t-tests comparing amplitude-values in the two conditions.
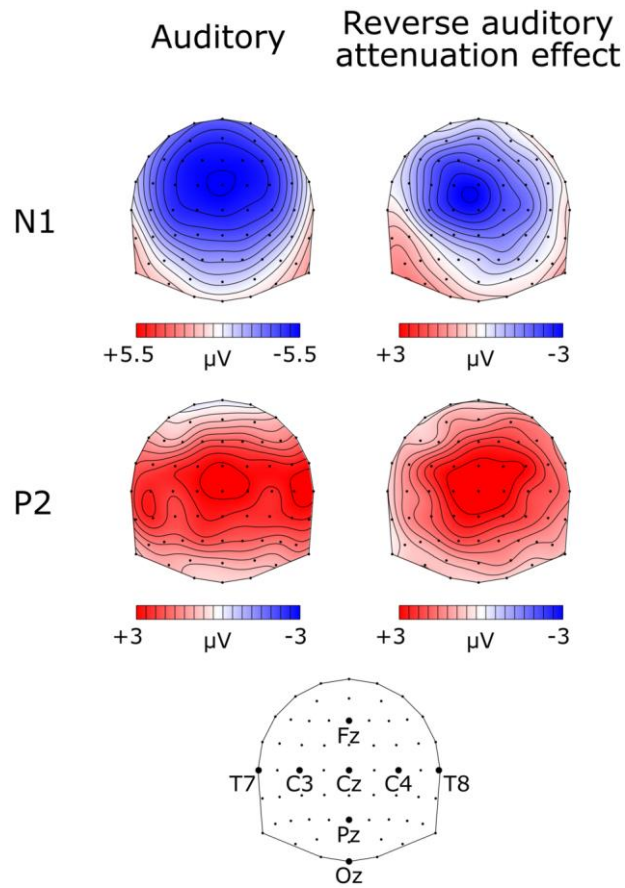
Figure 3. Group-average topographical distributions of the ERPs elicited by sine tones in the auditory condition and the corresponding reverse ERP attenuation effect (auditory minus motor corrected motor-auditory condition) in the N1 and P2 time-range. Note that signal ranges differ to allow the assessment of potential topographical shape differences (i.e., the scales symmetrically extend up to the maximal absolute amplitude in the topographies).
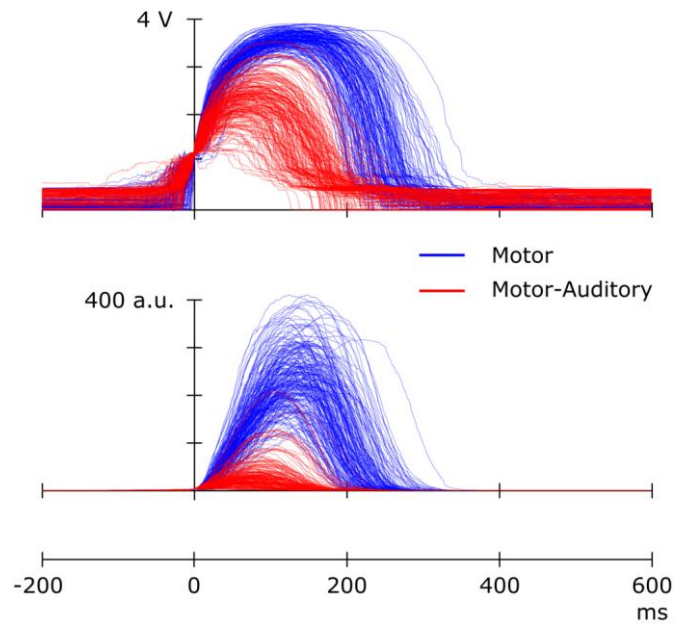
Figure 4. FSR-signal trajectories for all actions of a representative participant in the motor and motor-auditory conditions. The trajectories are synchronized to the time point (the crossing of the axes) at which the FSR signal exceeded a fixed threshold. On the bottom figure the same action profiles are depicted after transforming the FSR-signal to force values.
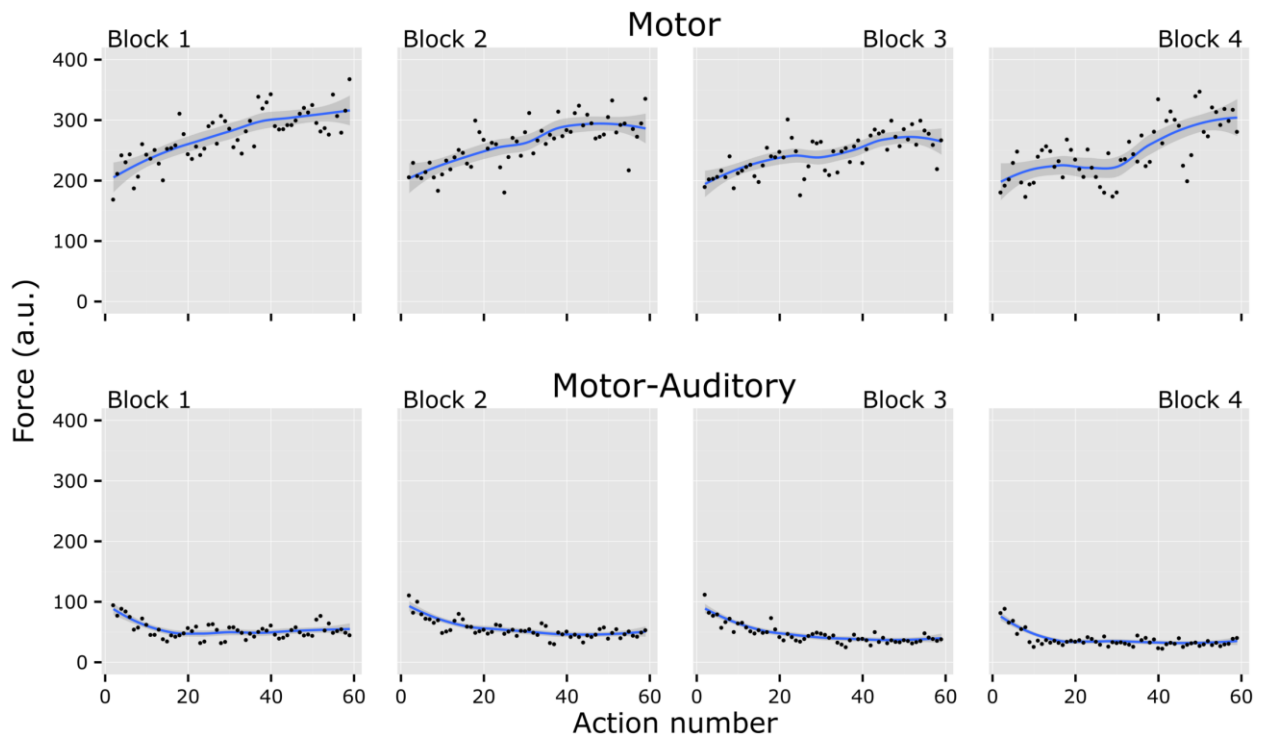
Figure 5. Group-average FSR-force peak amplitudes for each action, in each experimental

block (dots). The within-block trends are indicated by smooth curves (LOESS regression,

blue lines; the dark grey area represents the point-wise confidence intervals). Block numbers

represent the presentation order of blocks retained for analysis (see text). The presentation of

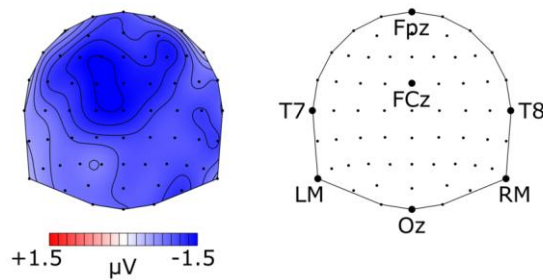motor and motor-auditory (and auditory) blocks was interwoven.
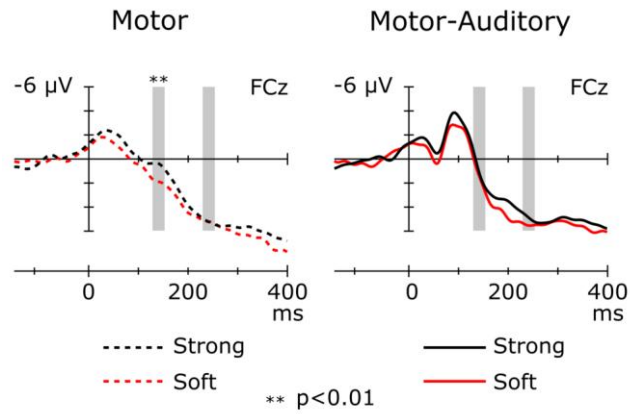
Figure 6. Top: ERPs related to strong (black lines) and soft (red lines) FSR-presses in the motor (top left) and motor-auditory (top right) conditions. Grey bars mark the 20 ms time-windows centered at the time-points of maximal N1- and P2 attenuations. Asterisks denote the significance levels of t-tests comparing ERP amplitudes related to strong and soft pinches in these intervals. Bottom: Group-average topographical distribution of the difference between ERPs related to strong and soft pinches in the motor condition, in the time-range of the maximal N1 attenuation.
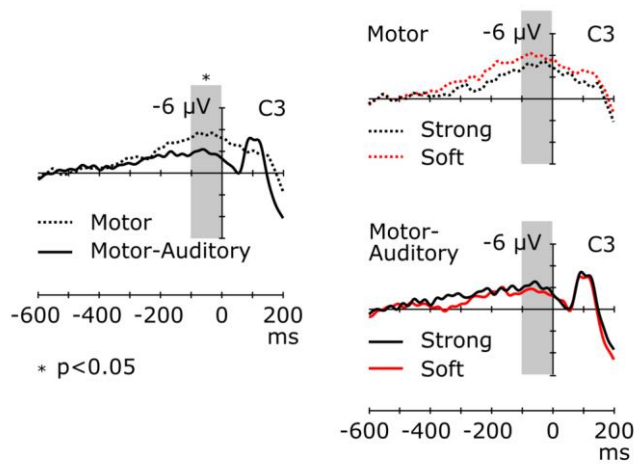
Figure 7. Group-average RPs at C3 in the motor and motor-auditory conditions (left). Group-average RPs related to strong and soft pinches in the motor (top right) and motor-auditory conditions (bottom right). Grey areas indicate the 100 ms time-windows for amplitude measurements. P-values show significance levels of two-tailed, paired Student's t-tests comparing amplitude-values in the motor and motor-auditory conditions (left) or amplitude measurements related to strong and soft pinches (right).

Consequences matter: self-induced tones are used as feedback to optimize tone-eliciting actions

Bence Neszmélyi, János Horváth

Supplementary material

Separation of the supra-temporal and modality-non-specific N1 sub-components

A secondary goal of the present experiment was to examine the contributions of auditory and modality-non-specific processes to the action-related attenuation of the N1 waveform. N1 comprises a number of overlapping components, including one which is generated in the supra-temporal cortex, and another presumably reflecting modality-non-specific processing (Näätänen & Picton, 1987). Although MEG studies indicate that action-related attenuation affects the supra-temporal component (Horváth et al., 2012; Martikainen et al. 2005), a recent study by San Miguel et al. (2013) suggested that in the ERPs, the attenuation of the modality-non-specific component is dominant. In their experiment, San Miguel et al. (2013) separated different sub-components of N1, and examined how self-induced actions affect these sub-components at different SOAs. They administered three conditions with isochronous action/tone-presentation rates (0.8 s, 1.6 s, 3.2 s) in separate experimental blocks. Action related ERP attenuation could be observed at the vertex for all presentation rates; the magnitude of the attenuation effect was, however, numerically the largest for the longest interval. Because with longer SOAs the relative contribution of the modality-non-specific component of the N1 waveform increases, this suggests that action related N1 attenuation was dominated by the attenuation of this sub-component.

In a previous (unpublished) study, we found that tones presented in band-limited noise in a tone-detection task elicited double-peaked N1 waveforms, with the first peak exhibiting a polarity inversion at the mastoids. Because of this, we assumed that presenting tones in noise

could be useful for separating the supra-temporal and the modality-non-specific N1 sub-components. By using this experimental setup in a classic auditory ERP attenuation paradigm, our goal was to test the conclusions of SanMiguel et al. (2013), as we hypothesized that separating supra-temporal and modality-non-specific components will make it possible to estimate the magnitude of the attenuation effect independently for these two N1 sub-components. Amplitude measurements were averaged in a 20 ms time-window around the peak of each sub-component and compared with two-tailed paired Student's t-tests. For the specific stimulation parameters see Methods.

Furthermore, because in the present study the participants' task was to produce a uniform SOA distribution in the 2 to 6 s range in each experimental block, the SOA dependence of the attenuation-effect could also be tested within the same condition. Here it was hypothesized, in accordance with the suggestion by SanMiguel et al. (2013), that the magnitude of attenuation would increase with longer SOAs. To test this, short- and long-SOA events were defined as the third of the trials with the shortest, and the third with the longest SOAs (for each participant in the motor-auditory condition). Both N1 (supra-temporal and modality-non-specific) sub-component- and P2 amplitudes were submitted to 2-way SOA (short, long) × condition ANOVAs. For this analysis, N1 and P2 amplitudes were calculated as signal averages in the 20 ms time-window centered on the negative (N1) and positive (P2) signal peaks in the group-average waveform for events with long SOAs in the auditory condition (at the electrode with the highest N1 and P2 amplitude respectively).

Results

Presenting the tones in band-limited noise did not yield the expected results, as double-peaked N1 waveforms could not be observed at the midline electrodes where action related ERP attenuation effects are usually measured (FCz, Cz). They were, however, evident

at more lateral sites (Figure S1.), with the most pronounced separation observable at C5 in the auditory condition. As the hypothesized double-peaked N1 was not observed at the vertex; however, the two peaks at C5 corresponded with the latency of the positive peak at the mastoid and the largest negative peak at the vertex, time-window for the N1 sub-components were determined according to these latter deflections. Significant ERP attenuation was found in the time-window centered at the peak in the mastoid signal: the amplitude was significantly lower (i.e. less positive at the mastoid, and less negative at the FCz) in the corrected motor-auditory waveform than in the auditory one, both in the mean mastoid signal ($t(15) = 3.042$, $p=.008$) and at FCz ($t(15) = -3.728$, $p=.002$). For the results regarding the attenuation of the N1 component at FCz see main text. These results replicate and extend the results of SanMiguel et al. (2013). The significant effect at the mastoid leads confirms that the supra-temporal N1 sub-component was attenuated when the tone was elicited by an action.

Participants complied with the instructions producing close to uniform SOA distributions in the 2-6 ms time-range. The variance in SOAs was 1.287 s in the motor and 1.174 s in the motor-auditory condition. This made it possible to select a set of actions (and corresponding tones) with long and short between action/stimulus intervals, and average the corresponding EEG epochs separately for each participant.

In contrast to the study of SanMiguel et al. (2013) the between-event (tone or action) interval had no effect on the magnitude of either the N1 amplitude or its attenuation. For the supra-temporal sub-component the SOA (short, long) × condition (corrected motor-auditory, auditory) ANOVAs of the amplitudes showed only significant condition main effects at FCz ($F(1,15) = 9.604$, $p = .007$, $\eta^2 = .171$) and the mastoids ($F(1,15) = 5.927$, $p = .028$, $\eta^2 = .110$), signaling action-related attenuation, but no main effect of SOA (at FCz: $F(1,15) = 0.022$, $p = .885$, $\eta^2 < .001$; at the mastoids: $F(1,15) = 2.200$, $p = .159$, $\eta^2 < .001$) or interaction (at FCz: $F(1,15) = 0.035$, $p = .854$, $\eta^2 < .001$; at the mastoids: $F(1,15) = 0.028$, $p = .871$, $\eta^2 <.001$) was

found. The same type of ANOVA of the modality-non-specific N1 amplitudes at FCz also showed only a significant condition main effect ($F(1,15) = 33.589$, $p < .001$, $\eta^2 = .318$), indicating action-related ERP attenuation, and no effects related to the between-event intervals could be observed (SOA main effect: $F(1,15) = 0.048$, $p = .830$, $\eta^2 < .001$; SOA × condition interaction: $F(1,15) = 0.016$, $p = .902$, $\eta^2 < .001$).

The SOA (short, long) × condition (corrected motor-auditory, auditory) ANOVA of the P2 amplitudes at Cz revealed only a condition main effect ($F(1,15) = 12.469$, $p = .003$, $\eta^2 = .231$), indicating action-related attenuation, but no significant SOA main effect ($F(1,15) = 0.142$, $p = .712$, $\eta^2 = .001$), or interaction ($F(1,15) = 0.414$, $p = .530$, $\eta^2 = .005$) was found.

The lack of SOA related effects could be simply explained by the fact that differences in N1 recovery should be larger for 0.8 and 3.2 s SOAs – reported in the experiment of SanMiguel et al. (2013) – than for 2.67 (mean for short SOAs) and 4.97 s (mean for long SOAs) between stimulus intervals featured in our experiment, despite the difference between the two SOA categories being of similar magnitude. Another cause for the absence of SOA based effects could be actions and stimuli with long and short intervals being featured within the same blocks. The increased variability in the SOAs (compared to tasks where participants have to perform the actions in an even tempo) could result in important changes both for actions in the motor, motor-auditory blocks (decreased rhythmicity and - possibly - increased attentional demands), and for sounds in the auditory condition (decreased temporal predictability), which may have also affected N1 amplitudes and the magnitude of the ERP attenuation effect (Lange, 2013).

References

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Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: A review and an analysis of the component structure. *Psychophysiology, 24*(4), 375–425. doi:10.1111/j.1469-8986.1987.tb00311.x

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Motor correction for self-induced sounds
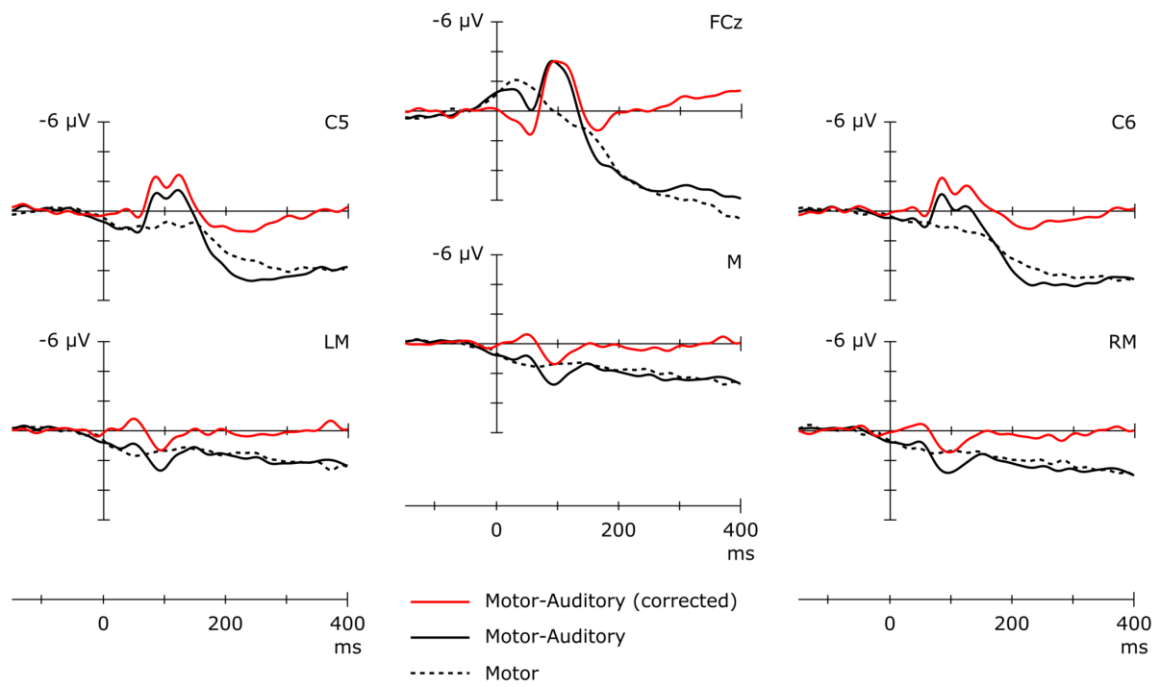
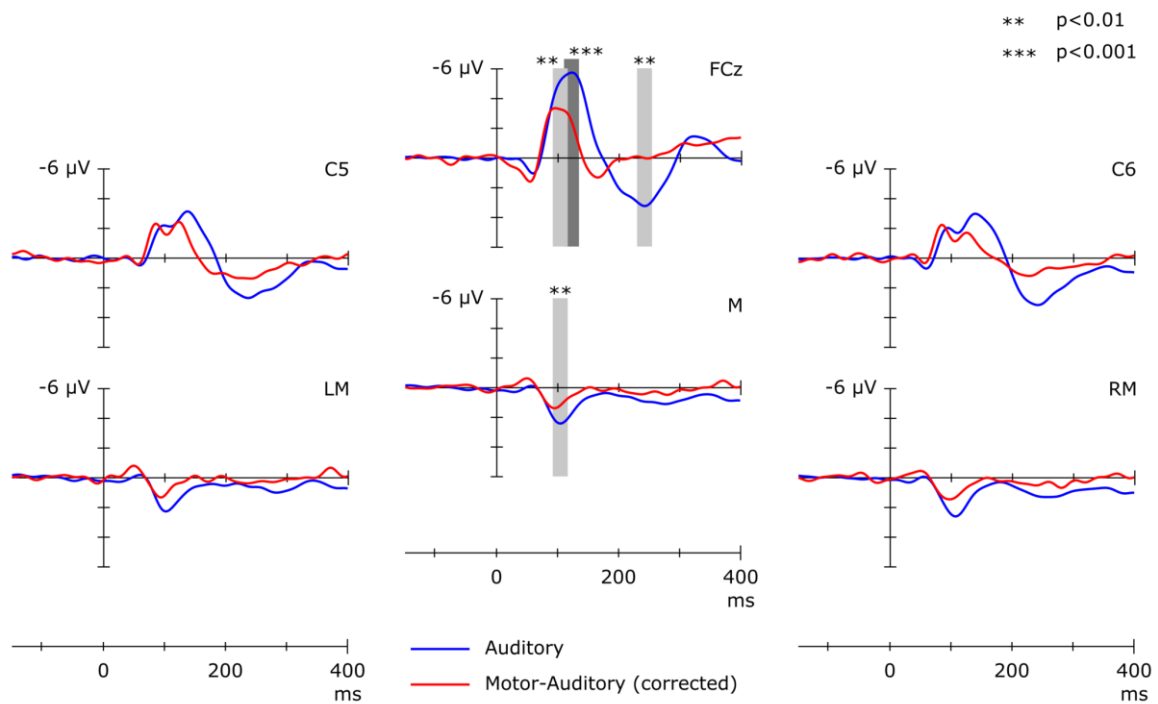## Auditory ERP attenuation for self-induced sounds

Figure S1. Group-averaged ERP waveforms elicited in the auditory, motor, and motor-auditory conditions at various electrodes. The figures on the top show the estimation of the auditory contribution to the ERPs elicited by compound action-sound events. The figures on the bottom display the group-average auditory and corrected motor-auditory waveforms. Gray bars mark the 20-ms time windows used for amplitude measurements. P values show significance levels of two-tailed, paired Student's *t* tests comparing amplitude values in the two conditions.