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Temporal constraints in the use of auditory action-effects for motor optimization

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Abstract

For quick ballistic movements the possibility of making online adjustments is limited. However, when the same action (e.g., pressing a button) is repeated multiple times, trial-bytrial adjustments are possible: Previous studies found that participants utilized auditory effects as feedback to optimize the applied force for such tone eliciting actions. In the current study, it was examined whether this *action-effect-related motor adaptation* also occurred if a delay was inserted between the action and its auditory effect. In two experiments, participants applied force impulses to a force-sensitive resistor in a self-paced schedule. Action–effect delay was manipulated between experimental blocks in the 0–1600 -ms range. The level of motor adaptation diminished as a function of action–effect delay, with no adaptation observable for delays longer than 200 ms, which indicates that action–effect contingency in itself is not sufficient to warrant that sensory effects will be useful for action control. A third experiment also showed that the observed temporal constraint was not absolute: Adaptation at 200-ms delay was stronger in a group of participants who were exposed to 400-ms action– tone delays before testing, than in a group exposed to a 0-ms action–tone delay, suggesting that action-effect-related motor adaptation is influenced by prior experience.

Keywords: action-effect-related motor adaptation, movement optimization, auditory feedback, self-induced sounds

Public significance statement

The study indicates that the temporal constraints of using auditory feedback for action control are much stricter than one would expect based simply on subjective experience. That is, there might be cases when one recognizes the causal connection between the action and its sensory consequence, however, the information provided by the stimulus still cannot be used for planning and controlling subsequent movements.

Introduction

Most everyday actions are strongly associated with a set of immediate sensory consequences. Switching on the lights, for example, leads to instant tactile (the sensation produced by applying pressure to the switch), auditory (clicking of the switch), and visual (the lights go on) effects. Indeed, actions are often performed with the goal to elicit such sensory effects (Elsner & Hommel, 2001; Hommel, 2009; Prinz, 1987). These sensory stimuli, however, are not only results of the actions, but are also important sources of feedback that can be utilized to optimize the movements (Adams, 1976; Ladwig, Sutter, & Müsseler, 2012; Todorov, 2004). The influence of sensory effects on motor control processes is reflected in movement initiation, as well as execution: Priming action effects allows for faster action initiation (resulting in faster responses, Elsner & Hommel, 2001, 2004; Hommel, 1996; Kunde, Koch & Hoffmann, 2004) and for increased action production rates (Elsner & Hommel, 2001; Pfister, Kiesel, & Hoffmann, 2011). Comparing expected action-effects with the actual sensory consequences also allows one to optimize the execution of the actions (i.e., to find the ideal trajectory or force, Todorov, 2004). A recent study (Neszmélyi, & Horváth, 2017) suggests that such optimization occurs even for simple, ballistic actions: It was found that adding a contingent, immediate auditory effect to a silent action (pinching a force sensitive resistor, FSR) led to the reduction of the applied force during interactions with the device. This was interpreted as a reflection of action-effect-related motor adaptation: The sound made it possible to decrease muscle effort while maintaining a reliable interaction with the device. Such an adaptation may depend on various characteristics of the action-effect relationship. The goal of the present study was to investigate the effect of action-effect delay on action-effect-related motor adaptation.

It seems straightforward to interpret force differences between actions with and without contingent auditory effects as the outcome of a strategic or quasi-strategic (depending

on the level of conscious awareness) optimization process. In the widely used paradigm (e.g., Baess, Horváth, Jacobsen, & Schröger, 2011; Ford, Palzes, Roach, & Mathalon, 2014; Martikainen, Kaneko, & Hari, 2005; SanMiguel, Todd, & Schröger, 2013; Schäfer & Marcus, 1973; Timm, SanMiguel, Saupe, & Schröger, 2013) administered by Neszmélyi and Horváth (2017) participants repeatedly interact with a device, performing the same action over and over again. Contingent auditory action-effects provide an opportunity to adjust actions in a trial-by-trial manner: According to the strategic account, the auditory effect informs participants that the action was successful, who consequently improve the effort/success ratio by reducing the force applied during subsequent actions. Theoretically, the only prerequisite of such an adaptation is that the causal action–effect relationship is represented by the cognitive system, which should be possible even with relatively long temporal delays (Buehner & McGregor, 2009; Shanks, Pearson, & Dickinson, 1989). Thus, if action-effectrelated motor adaptation is indeed a strategic process, force adjustments related to auditory feedback should be observable even if the sensory effect occurs a few seconds after the action was executed.

There are some experimental results that challenge the strategic account of actioneffect-related force adaptation: A number of studies investigating the effect of auditory feedback delay on the production of complex manual movement patterns at fast rates found that even small (i.e., 200–300 ms) delays disturbed both movement initiation and execution (playing a musical instrument: Finney, 1997; Gates & Bradshaw, & Nettleton, 1974; Pfordresher & Palmer, 2002, 2006; morse coding: Howell, Powell, & Khan, 1983; clapping: Kalmus, Denes, & Fry, 1955; or finger tapping Chase, Harvey, Standfast, Rapin, & Sutton, 1959, 1961; Finney & Warren, 2002). Although these studies focused primarily on movement-timing, it has also been observed that actions with delayed effects were stronger than actions with immediate effects. This force difference, however, may be brought about by

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several characteristics of these experiments. The guiding idea behind these studies was that delayed auditory stimuli disturbed pattern production, as the delayed sound stream interfered with the intended timing of the actions, and with the timing of the sensory feedback coming from other modalities (tactile, visual). This interference between different information streams provides a plausible explanation for disturbances in action timing when auditory effects are delayed. Consistent with timing effects, force differences between conditions with immediate and delayed auditory feedback might also arise from compensating with increased force in the delayed feedback condition for the interference caused by the delayed auditory effects. (That is, increased forces help to accentuate the actions, which makes it easier to keep track of the timing, and to produce precise movement patterns in conditions that are noisy due to the delayed stimuli.) However, force differences can be also interpreted in the optimization framework: Stronger forces for actions with delayed effects might indicate that there is a short time-window for using sensory effects as feedback for controlling the actions (Karlovich & Graham, 1966, 1967; Chase, 1965a, 1965b). This latter idea would be difficult to reconcile with the strategic account of action-effect-related motor adaptation, which assumes that force optimization relies exclusively on the representation of causality between the action and effect.

In the current study—similarly to previous delayed auditory feedback experiments the influence of action–effect delay on the physical characteristics of movements was investigated. However, effects of interference and feedback/optimization cannot be distinguished by tasks that require producing fast, complex movement patterns. Thus, we administered the paradigm previously used by Neszmélyi and Horváth (2017), which provides ideal circumstances for a strategic stepwise movement optimization, and reduces the possibility of interference caused by the delayed auditory effects: A single action (pinching an FSR) was repeated multiple times; the timing of the actions was freely determined by the

participant and did not adhere to a fixed rhythmic pattern; and between-action intervals were much longer than in previous experiments, thus action-effects did not overlap temporally with subsequent actions. These settings made it possible to assess "genuine" delay effects independently from interference phenomena. It was hypothesized that if action-effect-related adaptation relied on a strategic process, force optimization would be observable even at second-long delays (as far as causal connections could be readily recognized). On the other hand, if adaptation relied on a more "primitive" integration of action and effect, temporal constraints would be much stricter, and at long delays the feedback information provided by the auditory stimulus would have no influence on the execution of the actions.

Experiment 1

In the first experiment participants performed actions (pinching an FSR), which elicited sine tones with various delays in separate blocks (and there was a further control condition without auditory effects), in a time interval production task. In this experiment a 0-to 1600-ms range of action–effect delays was explored, as studies investigating motor– sensory interactions indicate that action–effect binding may happen with delays at least up until 1 s (Hommel & Elsner, 2004; Humphreys & Buehner, 2009; Shanks et al., 1989). The range of delays was selected by taking into account the range of acceptable between-action intervals (4–8 s, see below). Although the longest (1600-ms) delay was still relatively close to the 1-s limit referred to above, longer delays might have compromised the experiment, as participants could have used the sounds as reference points for the interval production task, which might have caused differences in attention attributed to the auditory stimuli, or lead to the formation of associations between the effect and the next action.

The logic of the experiment was that, if effect-dependent motor adjustment processes were limited to a certain delay-range, no optimization (i.e., force differences in comparison to actions without auditory consequences) should be observed for actions with auditory effects that fall outside that range.

Method

Participants

Twenty-eight healthy young adult students of the Eötvös Loránd University (age: 18– 24 years, female: 26, right handed: 27) participated in the experiment for course credit. Participants reported normal hearing and no history of psychiatric or neurological disorders. They gave written consent after the experimental procedures were explained. The experimental protocol (as well as those in Experiment 2, and 3, see below) conformed to the guidelines of the Declaration of Helsinki, and was approved by the United Ethical Review Committee for Research in Psychology (Hungary).

Stimuli, task procedure

During the experiment participants were seated comfortably in a sound proofed room. The experiment (as well as Experiment 2, and 3) was written and presented in Octave (Eaton, Bateman, Hauberg, & Wehbring, 2014), using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) provided by the NeuroDebian (Halchenko & Hanke, 2012) software repository.

Participants were instructed to apply brief force impulses to a thin force sensitive resistor (FSR 400, Interlink Electronics) fixed on a thin plastic sheet that they held between the thumb and the index finger (i.e. they were pinching the device, with the thumb positioned above). Participants were instructed to perform the actions—that is, apply pinch impulses—so

that between-action intervals within a block would show a uniform distribution in the 4–8 -s range. They were asked to try to distribute intervals randomly and not follow some systematic pattern. The uniform target distribution was selected to keep participants engaged in the task, and to reduce the automaticity of action generation (in contrast with tasks requiring the production of an even rhythm). The choice of between-action intervals also guaranteed that the delay between action and effect was considerably shorter than the interval between the effect and the next action.

Applying pressure changed the resistance of the FSR which resulted in a voltage change in the FSR-signal. When the signal exceeded a predetermined threshold (1.222 V corresponding to a force measure of 0.158 N) following a 10-ms interval in which the signal was continuously below the threshold, the response device registered an action.

In five conditions, administered in separate experimental blocks, the registration of an action was followed by the presentation of a sine tone (duration: 50 ms, including 10-ms linear rise and 10-ms linear fall times; frequency: 1000 Hz; intensity: 90 dB SPL; through HD-600 headphones, Sennheiser, Wedemark, Germany) with *delays of 0, 200, 400, 800,* or *1600 ms*. (Because of hardware limitations, beside the delays used in the description an additional 5-ms delay occurred in each condition.) Additionally, a *motor condition* was administered in a separate block, in which actions had no auditory effects.

The experiment was the second part of an experimental session consisting of two experiments (see, Figure 1). As the first experiment required the involvement of naïve participants with regards to the interaction with the response device, the use of the FSR was not practiced before starting the experiments. (The correct use of the device was demonstrated by the experimenter.) However, during the first part of the session participants had extensive experience with the FSR. As the elicited tone and the device settings (action-threshold) were

the same in both experiments, by the start of the experiment reported here, participants were already familiar with use of the FSR.

To familiarize themselves with the interval production task, participants performed short versions (25 trials) of the experimental blocks before the start of Experiment 1. In the first training block, feedback about action timing was immediate: a histogram of the betweenaction intervals with 1-s bins was presented on a screen, which was updated immediately after each action. In the second training block, such feedback was only provided at the end of the block. During these two training blocks, actions elicited no auditory effects.

After the training phase, participants performed the six experimental blocks (one for each condition). The blocks were presented in random order, with short (1 minute) breaks between them. Each block consisted of 50 trials. At the end of each block, participants received feedback on their performance: As in the second training block, a histogram of the between-action intervals was presented on the screen.

Data acquisition

The FSR-signal was recorded with a Synamp2 EEG amplifier (Compumedics Neuroscan, Victoria, Australia), on its high-level input channel, with a sampling rate of 1000 Hz (online low-pass filtered at 200 Hz, i.e. DC-200 Hz range). Before analysis, the signal was transformed to force values by applying an exponential transformation (Interlink Electronics, 2016). 2-s epochs (1 s pre- and 1 s postaction), time-locked to the crossing of the FSRthreshold, were extracted from the continuous FSR-signal. Epochs were discarded if another action was present in the 1 s preceding or the 0.5 s following the action. Results of a previous study (Neszmélyi & Horváth, 2017) suggest that the first few pinches in a block might be used for a stepwise optimization of the interaction with the device, thus the first 10 epochs of each block were discarded, as in the current experiment a comparison of the stabilized forcesets was aspired to rather than the exploration of the adjustment phase.

Data analysis

Mean between-action intervals were calculated for each participant in each condition, which were submitted to a one-way repeated measures analysis of variance (ANOVA).

Actions were characterized in two ways. First, as in the study by Neszmélyi and Horváth (2017) each action was characterized by the maximal force signal in the 800 ms following the crossing of the force threshold. For each participant, in each condition, the median of the pinch forces in the given condition was determined. The differences between conditions were explored by pairwise Wilcoxon signed-rank tests (with Holm correction). Effect sizes are reported as rank biserial correlations (King, Rosopa, & Minium, 2011; Kerby, 2014). Statistical analyses were conducted in R (version 3.0.2., R core team, 2015), figures were designed using the ggplot2 package (Wickham, 2009). Second, because peak force may be influenced by online motor control processes responding to the onset of the elicited tones, the same analyses were also conducted for the impulse (integral of the force signal) measured in the 10—60-ms interval. It is unlikely that force parameters would be adjusted within 60 ms of the onset of the elicited tone, thus this measure should reflect differences in action planning only. Analyses using the force impulse measure, and further considerations regarding the contribution of online control mechanisms to action-effect-related motor adaptation are presented in the Supplementary material.

Force values for actions with and without auditory effects obtained in a precursor experiment (Neszmélyi & Horváth, 2017) were submitted to a Wilcoxon signed-rank test (in the original paper actions were compared by paired Student's *t*-test). The analysis yielded T = 0, p < .001 corresponding to an effect size of 1 (matched-pairs rank biserial correlation

coefficient, King et al., 2011; Kerby, 2014). At an alpha level of .003 (alpha level of .05 corrected for 15 pairwise comparisons), a sample size of 6 is sufficient to reveal an effect of this magnitude with a statistical power of 80%. The precursor study, however, only shows the influence of immediate auditory effects on actions executed with the FSR. Whether delayed action consequences would show effects of similar magnitude, was not known before the current experiment. With the sample size used in the study (28 participants), effect sizes higher than .638 (corresponding to *T*s below 73.580) can be detected with a statistical power of at least 80%.

Results

Participants complied with the instructions, as most between-action intervals fell into the 4–8-s range (Figure 2.). The one-way ANOVA comparing individual mean betweenaction intervals across conditions showed no significant effect.

The auditory effect significantly influenced the applied force only if it followed the action within 200 ms (Table 1, Figure 3). The applied forces did not significantly differ from that in the motor condition for delays longer than 200 ms.

Discussion

The results of Experiment 1 indicated that there was indeed a temporal action–effect delay limit for action-effect-related motor adaptation. Only self-induced tones following the actions with a delay no longer than 200 ms contributed significantly to action-effect-related motor adaptation. (Although, even motor adaptation with 200-ms delays was not nearly as efficient as in the case of auditory effects with no delay.) For longer delays, no motor adaptation could be observed: Actions that elicited auditory effects with a delay of 400 ms, or more, did not differ significantly from actions with no extrinsic effects. The observed time-window for action-effect-related motor adaptation is substantially shorter than the temporal

constraints for causality judgements or for sensory-motor interactions that supposedly rely on causal relations (e.g., ideomotor action control: Elsner & Hommel, 2004, intentional binding: Humphreys & Buehner, 2009). According to our initial hypothesis, this indicates that actioneffect-related motor adaptation is not a strategic process, and requires a different form of action–effect integration, than phenomena based on causal representations.

The dependency of motor adaptation on action–effect delay reported in this study is similar to those observed in rhythmic tapping experiments (Chase et al., 1959, 1961; Chase, Rapin, Gilden, Sutton, & Guilfoyle, 1961; Finney & Warren, 2002; Karlovich & Graham, 1966, 1967; Ruhm & Cooper, 1963, 1964). Whereas in those studies force differences between conditions with immediate and delayed feedback could also be attributed to interference between different information sources (action execution, tactile feedback, auditory feedback), in the current study, potential contributions of similar interference effects can be considered insignificant, and the observed force differences can be attributed to auditory action-effects losing their feedback-function with increasing action–tone delay. Indeed, it seems possible that the decreasing action–effect integration with longer delays observed in the present study might have contributed to force-increases in the cited rhythmic tapping studies (Karlovich & Graham, 1966, 1967; Chase, 1965a,b).

It has to be noted that the delay effects observed in the experiment could be also plausibly explained by referring to online control mechanisms (i.e., an immediate reaction to the sensory stimulus): If participants increase pressure until the auditory effect signals that the action was successful, stimuli presented with a short delay can result in earlier release of the device and thus in reduced forces. (Release might be also initiated if tactile stimulation reaches a certain level, even if auditory effects are not elicited, which could explain how releasing the device is induced in the motor condition.) However, based on previous studies (Horváth, Bíró, & Neszmélyi, in press) and additional analyses of the current results (see

Supplementary material) it seems likely that the tone eliciting movements used in the current study can be indeed regarded as ballistic and action-effect-related motor adaptation is mainly determined by offline mechanisms of action planning. Thus, in the following, we focus on explanations that are related to such offline processes, and the potential contribution of online control is discussed in the Supplementary material.

It is also important to consider that Experiment 1 was administered immediately after participants completed another experiment (not reported in the current study), which investigated processes of action-effect-related motor adaptation in a between-group arrangement (see Figure 1). Although a short break and additional training blocks were inserted between the two experiments, participants assigned to different groups in the preceding experiment had different experiences at the onset of Experiment 1. As the results of a later experiment (Experiment 3, below) indicated that differences in prior experience may influence action-effect-related motor adaptation, the results of Experiment 1 could have been affected by carry-over effects. To test this possibility, participants in Experiment 1 were divided into groups according to their group assignments in the preceding experiment, and applied force was compared between these groups in each condition. Also, all force analyses related to Experiment 1 were performed separately for the two groups. The results did not indicate any carry-over effects: Pinch forces did not differ for the two groups in any of the six conditions. Also, the pattern of delay effects described above was clearly observable in both groups (see Supplementary material).

Experiment 2

The results of Experiment 1 indicate that the usefulness of auditory action-effects for motor adaptation ceases with action–effect delays longer than ca. 200 ms. The goal of

Experiment 2 was to replicate these results, and provide a picture of this effect with a finer temporal resolution in the 0- to 200-ms action–effect delay range.

Method

Participants

Twenty-eight healthy young adult students of the Eötvös Loránd University participated in the experiment. None of them took part in Experiment 1. The students received course credit for participation. They reported normal hearing and no history of psychiatric or neurological disorders, and gave written informed consent after the experimental procedures were explained. Because of device malfunction, one dataset was excluded from the analysis. The final sample consisted of 27 participants (aged: 18–25, female: 20, right handed: 22).

Stimuli, task, procedure

The experimental design was identical to that of Experiment 1, with three exceptions: First, *delays of 0, 50, 100,* and *200 ms* were utilized. (Due to hardware limitations, the actual delays were 5 ms longer in each condition, as in Experiment 1). Second, as action–effect delays were shorter than in Experiment 1, target between-action interval was shortened to 2–6 s. (We assumed that this would still not lead to substantial interference between the auditory effect and the following action.) Third, the intensity of the auditory effect (i.e., the 1000 Hz, 50-ms sine tone) was 75 dB SPL.

Similarly to Experiment 1, Experiment 2 was also the second part of an experimental session consisting of two experiments (Figure 4). In the first part of the session (reported as Experiment 3 in the current study), participants were familiarized, and had extensive experience with the device (see Experiment 3, below). After finishing this first experiment, participants performed a practice block to familiarize themselves with the interval production

task. This was the same as the interval production practice for Experiment 1 (immediate feedback about the produced intervals, and no auditory effects elicited by the actions), with temporal parameters adjusted to the task in Experiment 2 (i.e., 2–6-s time range).

Data acquisition, data analysis

Data acquisition and analysis was the same as in Experiment 1. To correct for potential violations of the sphericity assumption in the one-way ANOVA of the mean between-action intervals, Greenhouse-Geisser correction was applied (uncorrected degrees of freedom, the ε correction factor, and corrected p-values are reported). To follow-up the significant ANOVA effect, pairwise Student's *t*-tests were used. (As in the case of Experiment 1, analyses using the force impulse measure are reported in the Supplementary material.)

Although the influence of action–effect delays shorter than 200 ms were not assessed previously, it could be assumed that the effects will not be smaller than observed in the 200ms delay condition of Experiment 1. The comparison of the motor and 200-ms delay conditions in Experiment 1 (see Experiment 1 Results) yielded an effect size of .788, for which a sample size of 15 is sufficient to reveal an effect with a statistical power of 80% at an alpha level of .005 (.05 corrected for 10 pairwise comparisons). With the sample size used in the study (27 participants), effect sizes higher than .630 (corresponding to *T*s below 69.882) can be detected with a statistical power of at least 80%.

Results

Participants were successful in keeping between-action intervals in the 2–6-s range (Figure 5). The ANOVA comparing the (individual) mean between-action intervals indicated a significant effect: F(4,104) = 7.686, $\varepsilon = .605$, p < .001, $\eta^2 = .143$). Pairwise paired *t*-tests showed that between-action intervals in the motor condition were significantly longer than in

any other condition. (motor – 0-ms delay: t(26) = 3.275, p = .003, d = 0.630; motor – 50-ms delay: t(26) = 3.982, p < .001, d = 0.766; motor – 100-ms delay: t(26) = 2.947, p = .007, d = 0.567; motor – 200-ms delay: t(26) = 3.149, p = .004, d = 0.606), but there were no significant differences between conditions with auditory feedback.

The applied force gradually increased as a function of action–effect delay, that is, force optimization decreased with the delay (Table 2, Figure 6). Confirming the results of Experiment 1, the auditory effect can be used to optimize the eliciting action up to a delay of at least 200 ms.

Discussion

Experiment 2 showed that in the 0–200-ms delay range action-effect-related motor adaptation decreased gradually with increasing action–effect delay. Interestingly, even at the shortest delays (50 ms), the level of adaptation was reduced by the action–effect interval. In the case of manually elicited sounds, a delay of 100 ms is usually not recognized by participants (Elijah, Pelley, & Whitford, 2016). Thus, it seems that similarly to perceptual processing of self-induced sounds (Aliu, Houde & Nagarjan, 2009; Cao, Veniero, Thut, & Gross, 2017; Oestreich et al., 2016; Whitford et al., 2011; Stetson, Cui, Montague, & Eagleman, 2006), motor processes can also be affected by delaying the sensory consequences of the actions, even when the delays are not consciously recognized.

It is important to note that similarly to Experiment 1, Experiment 2 was also administered immediately after participants completed another experiment that applied a between-group design (Experiment 3). Therefore, Experiment 2 was also tested for carryover effects. The same method was applied as in Experiment 1: Participants were divided into two groups, according to their assignment in Experiment 3. Applied force was compared between the groups in each condition, and all force analyses related to Experiment 2 were

performed separately for the two groups. The results showed that a carry-over effect was indeed present, but the pattern of delay effects described above was clearly observable in both groups (see Supplementary material). That is, the carry-over effects did not substantially affect the main findings of Experiment 2.

Experiment 3

Experiment 1 and 2 showed that the delay between action and its auditory effect influenced the level of force adaptation for tone-eliciting actions, that is, the use of auditory effects for action control was subject to temporal constraints. From these experiments, it remained, however, unclear whether these constraints were absolute, or depended on other factors. Experience with different action–effect delays seems to affect other types of sensory– motor interactions (Aliu et al., 2009; Cao et al., 2017; Elijah et al., 2016; Stetson et al., 2006). The goal of Experiment 3 was to examine whether action–effect-related motor adaptation is also influenced by previous experience with action–effect conjunctions.

Although the temporal constraints of force optimization observed in Experiment 1 and 2 suggest that causal representation acquired by associative learning mechanisms are not sufficient for action-effect-related motor adaptation, this interpretation relies on the assumption that a strong causal action–effect association was also present in conditions with long action–effect delays (i.e., 400 ms and longer). Although this seems likely, the possibility cannot be excluded that the delay-related differences in action-effect-related motor adaptation reflect some gradual change in the acquisition of causal action–effect association (which might not even be captured in the subjective experience). That is, at longer delays such associations might be weaker, or might be established more slowly. Experiment 3 aimed to investigate this possibility, without relying on participant's subjective reports. We assumed

that if optimization relied on acquiring causal associations, extensive experience with action– effect conjunctions could result in a form of hysteresis: Binding the action and a delayed effect might be easier if the causal relationship between the two events was already established previously in a condition where the action was immediately followed by the auditory consequence.

Two groups of participants, who had no prior experience with the device used in the study, were adapted either to an action–effect delay of 0 ms, or 400 ms. Following the adaptation period, in the test condition both groups performed actions with a 200-ms action– effect delay. It seems plausible that the group exposed to a 0-ms action–tone delay had a better opportunity to establish an action–effect association than the group performing actions with a 400-ms delay. If action-effect-related motor optimization relied on such an association, one would expect that the 0-ms delay-adapted group would show a better performance (i.e., a force level closer to the optimum) in the following 200-ms test condition, because they had a better opportunity to establish the action–effect association.

Method

Participants

The sample in Experiment 3 was the same as in Experiment 2. Participants completed the two experiments in one session (starting with Experiment 3).

Stimuli, task, procedure

At the beginning of the experimental session, participants learned about the force level necessary to produce actions that are registered as such by the device. They were instructed to apply various amounts of pinch force to the device and the corresponding signal was continuously displayed on a screen in the form of a blue vertical bar that changed its length as a monotonic function of the force. When the applied force was above the threshold, the color of the bar turned green. Participants were encouraged to explore how the visual representation of the signal changed during the interaction with the device.

The experimental setup was the same as in Experiment 2, with the exception of the interval production task: Here participants were instructed to perform the actions at a constant pace (once every 3 s). To familiarize themselves with this interval production task, participants completed a short training block (30 trials). In the training block feedback about action timing was immediate: After each action, the duration of the last between-action interval was displayed on the screen. During the training block, actions did not elicit auditory effects.

The experiment consisted of four blocks with different action-effect delays. The interval production task was the same for all blocks. First, participants completed a motor block. This was similar to the training block: Actions did not elicit auditory effects. However, the block was longer (60 trials, ca. 3 minutes) and—as in all experimental blocks participants only received feedback about the interval production task at the end of the block. Second, in a long (180 trials, ca. 9 minutes) adaptation block, participants were adapted to a certain action-effect delay. Participants were divided into two groups. For one group, auditory effects followed the actions with a delay of 0 ms (N = 14, aged: 18–25, female: 9, right handed: 12). For the other group, the action–effect delay was 400 ms (N = 13, aged: 20–24, female: 11, right handed: 10). The third block was the *test* block (60 trials, ca. 3 minutes). During this, the action-effect delay was 200 ms for both groups. The test block was started immediately after the adaptation block was finished, however, as stimulus presentation and data recording programs had to be started, there was a short delay between the two blocks. This delay before the test block was not significantly different for the two groups (0-ms delay adapted: M = 32.357 s, SD = 10.696 s; 400-ms delay adapted: M = 28.214 s, SD = 4.061 s). Finally, participants completed a *control* block. During this, action–effect delays were

reversed for the two groups (compared to the adaptation block): the 0-ms delay adapted group performed actions with 400-ms action–effect delays, while auditory effects were delayed by 0-ms for the 400-ms delay adapted group. (As in the previous experiments, because of hardware limitations, the actual delays were in all cases longer by 5 ms than indicted in the description of the task.)

Data acquisition

Recording and preprocessing (epoch selection, and rejection criteria) of the FSRsignal was the same as in Experiments 1 and 2, except the first trials of the blocks were not discarded.

Data analysis

Individual between-action intervals in the four conditions were measured as in Experiments 1 and 2. As the task differed for the two groups in two of the four conditions (different action–effect delays in the adaptation and control conditions), the between-action intervals for the groups were analyzed separately. The individual between-action intervals were submitted to two one-way repeated measures ANOVAs (with Greenhouse-Geisser correction, as described above). Differences were further explored by pairwise paired samples Student's *t*-tests. The force applied by each participant in a given condition was characterized as in the other two experiments: by the median of the peak pinch forces produced by the participant in that condition.

The main question of the experiment was whether there was a difference in applied force between the two groups in the test block. To test this, individual force values of the two groups were submitted to a Wilcoxon rank-sum test. To assess further differences induced by adaptation to different action–effect delays, between-group differences (in pinch forces) in the other three conditions were also examined by Wilcoxon rank-sum tests. To estimate effect sizes for the between group comparisons non-directional rank biserial correlations were calculated, using the Wendt formula (Kerby, 2014).

Because the adaptation block comprised more than three times as many actions as the blocks in Experiment 1 and 2, we also performed an exploratory analysis of the time-course of the optimization. The adaptation block was divided into three parts. Median pinch forces in each block part were calculated for each participant. To examine if force differences between the 400-ms and 0-ms delay still persisted after longer practice, pinch forces were compared between groups for each block part using Wilcoxon rank-sum tests. The forces between block parts were also compared by Friedman's test, separately for the two groups. Significant differences were followed up by pairwise Wilcoxon signed-rank tests.

Results

The repeated measures ANOVAs of the between-action intervals (Table 3) showed significant condition effects in both groups (0-ms delay adapted group: F(3,39) = 3.763, $\varepsilon = .661$, p = .037, $\eta^2 = 0.183$; 400-ms delay adapted group: F(3,36) = 8.213, $\varepsilon = .597$, p = .003, $\eta^2 = 0.286$). As in Experiment 2, the condition effect was caused by longer between-action intervals in the motor in comparison to those in the other blocks, the between-action intervals in the conditions with auditory effects did not differ significantly: In the 400-ms delay-adapted group, between-action intervals in the motor condition were significantly longer than in any other condition (motor-adaptation (400-ms delay): t(12) = 3.774, p = .003, d = 1.047; motor-test (200-ms delay): t(12) = 2.967, p = .012, d = 0.823; motor-control (0-ms delay): t(12)=3.601, p = .004, d = 0.999), and similar differences could also be observed in the 0-ms delay-adapted group (motor-adaptation (0-ms delay): t(13) = 2.408, p = .032, d = 0.644; motor-test (200-ms delay): t(13) = 2.676, p = .019, d = 0.715; motor-control (0-ms delay): t(13) = 2.477, p = .028, d = 0.662).

As shown in Figure 7, in the test block, actions were significantly stronger in the 0-ms delay adapted group than in the 400-ms delay adapted group (U = 36, p = .007, r = .604). This is the opposite of that observed in the adaptation blocks themselves, in which—corresponding with the influences of action–effect delay observed in Experiment 1—the no-delay group was characterized by a more pronounced optimization (i.e., softer actions, U = 34, p = .005, r = .626). In the motor condition, there was no significant difference between the two groups (U = 64, p = .202, r = .297). There was a significant difference between the two groups in the control condition (U = 8, p < .001, r = .912): Participants who in this phase elicited tones with 400-ms delays applied more force during actions than those who were performing actions that were immediately followed by the auditory stimulus. Note that between-group differences in the control block cannot be unambiguously interpreted, because in this block, action–effect delays differed for the two groups. Also, adaptation to different action–effect delays established previously might have still persisted at this point. However, the difference between the two groups is consistent with the influence of delay on action-optimization that was observed in Experiment 1 and 2.

As shown in Figure 8, in the adaptation block, force-differences between the two groups were significant in the first (U = 28, p = .002, r = .692), second (U = 44, p = .022, r = .516), and also in the third (U = 46, p = .029, r = .495) block part. This suggests that even at the end of a ca. 9 minute long adaptation period, optimization still did not reach the level of optimization achieved with zero action–effect delay. The Friedman's tests comparing force values showed a significant block-part effect for the 400-ms delay adapted group ($\chi^2(2) = 9.846$, p = 0.007), as well as for the 0-ms delay-adapted group ($\chi^2(2) = 8.714$, p = .013), that is, the level of optimization changed during the adaptation block in both groups. In the group adapted to 400-ms delay, pairwise comparisons showed significant differences between all block-parts (1st and 2nd: T = 16, p = .040, r = .648; 1st and 3rd: T = 4, p = .002, r = .912; 2nd

and 3^{rd} : T = 11, p = .013, r = .758), indicating a gradual, but consistent optimization during the block. For the 0-ms delay-adapted group the applied force was significantly stronger in the first than in the third (T = 15, p = .017, r = .714), and marginally stronger than in the second (T = 25, p = .091, r = .524) part. There was, however, no significant difference between the second and third block parts, suggesting that for this group optimization happened faster, at the beginning of the block.

Discussion

The results confirmed that action-effect-related motor adaptation was affected by previous experience with action–effect conjunctions: Participants who trained with a longer (400-ms) action–effect delay were better in using a less (200-ms) delayed auditory effect for optimizing their motor act, than those who were first adapted to an interaction with immediate effects. Consistent with studies about sensory attenuation (Cao et al., 2017; Elijah et al., 2016) and action effect reversal (Stetson et al., 2006), these results indicate that the temporal constraints of action–effect integration underlying action-effect-related motor adaptation are not absolute, but depend on prior experience.

On the one hand, the effect of experience was the opposite of what could be expected based on the associative learning framework. It seems that establishing stronger action–effect associations by having experience with immediate auditory action-effects did not contribute to better force optimization at an intermediate delay. On the contrary: Experience with longer delays (400 ms) led to more pronounced optimization in the 200-ms delay test block. This might confirm the interpretation of Experiment 1, that action-effect-related motor optimization is not a strategic process relying on causal action–effect representations (see General discussion).

On the other hand, within-block tendencies observed in the experiment might rather support the interpretation that action-effect related motor adaptation is related to establishing causal associations, and the delay-related differences in optimization (as observed in Experiment 1) only reflect different time-course for establishing action–effect associations with short and long delays. Explorative analysis of force development in the 9-min adaptation block expanded on the results of the first two experiments, by indicating that the 200-ms limit for action-effect-related motor adaptation is not absolute: It seems, that given sufficient practice, motor adaptation could also occur with action–effect delays longer than 200-ms. (Although, after 180 action repetitions performed in ca. 9 minutes, there was still a significant force difference between participants performing actions with immediate and 400-ms delayed auditory effects. This might mean that even after extended practice, action control is less effective when relying on substantially delayed auditory effects, but it could also indicate that adaptation was still in progress at the end of the adaptation period.)

The associative account might also provide an explanation for the influence of experience on subsequent interactions with a device. Causal judgements have been shown to depend on previously experienced action–effect delays, extended practice with longer action– effect delays can "overwrite" expectations of immediate effects (Buehner & May, 2004; Buehner & McGregor, 2006). Similarly for action-effect-related motor adaptation: More effective optimization in the test condition (200-ms delay) by the 400-ms delay adapted group might be explained by those participants already having established expectations for delayed auditory effects (instead of immediate ones), or by them being trained in association-forming with a longer interval between action and sensory effect. This interpretation presupposes that the fast force optimization with short and the slow optimization with long action–effect delays reflect the same process. However, it could also be argued that these are two separate phenomena (see General discussion).

It is important to note that the task in Experiment 3 (constant interval production) differed from those in Experiment 1 and 2 (random interval production). Action-effect-related motor adaptation has been observed previously with both of these tasks (Neszmélyi & Horváth, 2017; Horváth, Bíró, & Neszmélyi, in press), but we are unaware of any studies investigating potential task-related differences. Currently no results indicate that tendencies observed in any of the three experiments would be specific to the respective task. Indeed, results of Experiment 3 are consistent with those of Experiment 1 and 2: For both Experimental groups force values in the 200 ms-delay condition were similar in Experiment 2 and 3. Also, in Experiment 3 during the first block part of the 400-ms delay adaptation block (first 60 trials) forces were not significantly different from those in the motor block (consistent with the results of Experiment 1 in which one block included 50 trials). The slow adaptation that was observed during the course of the block is more likely a result of extended exposure than some effect related to the interval production task.

General discussion

The present study showed that despite a fully contingent action–effect relationship, action-effect-related motor adaptation was constrained by the delay between the action and its auditory effect. The experiments showed that the magnitude of adaptation fell off with increasing delays. In Experiment 1 and 2, a gradual decrease in force adaptation could be observed, with no significant adaptation for delays over 200 ms. The results of Experiment 3 showed, however, that this 200-ms temporal boundary was not absolute: Following a prolonged exposure to a longer (400 ms) action–effect delay resulted in significant motor adaptation in a 200-ms delay test condition in contrast with the case when the 200-ms delay test condition followed a similar exposure to a zero-delay action–tone contingency.

We previously hypothesized (Horváth, Bíró, & Neszmélyi, in press; Neszmélyi & Horváth, 2017) that action-effect-related motor adaptation reflected the agent's ability to rely on sensory effects, and utilize them as signals of action-success. That is, in the case of an action-tone contingency, the sound signaled that the interaction has actually happened as intended. The present study challenges this purely strategic interpretation of action-effect-related motor adaptation: The experiments demonstrate that the causal action-effect related motor adaptation: The experiments demonstrate that the causal action-effect relationship is not sufficient for motor adaptation. Although we did not measure causality or agency judgements, it seems obvious that even at the longest—1600 ms—delay, the connection between action and effect was easily recognizable. That is, even though participants are aware that the just-performed action was successful, their capability to optimize the motor parameters of their forthcoming action decreases as the delay between the action and its auditory effect grows. Indeed, in Experiment 1, at delays longer than 200 ms, no motor adjustments were observable at all.

The present results seem to suggest that action-effect-related motor adaptation has a more strict temporal constraint than some other action–effect integration phenomena. The 200-ms limit is much shorter than the few seconds long time-window reported in studies investigating phenomena related to causal connections (Hommel & Elsner, 2004; Humphreys & Buehner, 2009; Shanks et al., 1989), but it is similar to those reported for action-related sensory attenuation or action–effect reversal (Cao et al., 2017; Oestreich et al., 2016; Stetson et al., 2006; Whitford et al., 2011). This suggests that—similarly to these latter phenomena—action-effect-related motor adaptation might rely on a form of action–effect integration which is different from causal representations acquired by associative learning mechanisms.

The present study addressed only the question whether there were any temporal constraints for action-effect-related motor adaptation. Nonetheless, several speculations can be put forward on the underlying causes of the observed delay effects. The general idea,

outlined in the previous paragraphs, which explains the delay effects with a time limit for automatic action-effect binding, can be integrated into various theories on action planning and control. On the one hand, within the ideomotor framework (Elsner & Hommel, 2001; Hommel, 2004, 2009; Kunde, Koch, & Hoffmann, 2004; Prinz, 1987)-which focuses on the predictive aspect of motor control, emphasizing the role of goals and expectations in action planning-the lack of action-effect binding in the case of long action-effect delays could mean that auditory stimuli outside a certain time window are not integrated into the action representations. The ideomotor theory suggests, that action planning is driven by the sensory effects that have been integrated into the action representation, thus, it is plausible to assume that action planning is more efficient in cases where distinctive external effects are linked to the actions. If action-sound binding is compromised when the interval between the two events is too long, only less reliable feedback modalities (i.e., tactile, proprioceptive) can be utilized for action control, which would explain the lack of optimization for delays above 200 ms. On the other hand, the close connection between optimization processes and action-effect binding fits equally well with computational theories of action control (Adams, 1976; Franklin & Wolpert, 2011; Todorov, 2004; Wolpert, Diedrichsen, & Flanagan, 2011; Wolpert & Ghahramani, 2000). Even if action goals are not attributed a significant role in planning the movements, the lack of action-effect binding could compromise a retrospective evaluation of movements and thus the planning and execution of subsequent actions. That is, if the auditory stimulus is not linked to the preceding movement it will not affect the evaluation of actionsuccess, and parameters of subsequent actions will be determined similarly to actions that have no distinctive auditory consequences (i.e., actions in the motor condition).

Both explanations above suggest that action optimization does not happen at longer delays because the actions and the elicited auditory stimuli are not bound together in representations that govern action planning and control (although the causal relationship

between the two events can be most likely recognized.) Thus, action control strategies (and as a result physical properties of the actions) resemble the case when auditory effects are completely absent. However, an alternate explanation, which does not rely on action–effect binding being compromised by long delays, can also be put forward: Kunde and colleagues (2004) suggested that during action planning, agents strive for a certain level of combined feedback intensity - a weighted sum of all available feedback sources. If the intensity of one source of feedback is decreased, actions will be adjusted to increase feedback intensity from other sources. According to this theory action-effect-related motor adaptation (i.e., force difference between actions with and without distinctive auditory effects) might be caused by participants increasing tactile stimulation intensity when auditory effects are omitted. Delay effects in the current experiment could be explained by assuming that the weight of a sensory effect in the combined overall feedback intensity decreases with temporal delay. That is, when auditory feedback is delayed, its contribution to the combined overall feedback intensity decreases, which participants compensate by increasing the applied force in order to increase the contribution of tactile feedback intensity.

One might also argue that the apparent 200-ms limit could actually be brought about by the block duration choices implemented in the experimental paradigm. That is, because in Experiment 1 and 2 exposures to different action–effect delays were relatively brief (i.e., ca. 5 and 3.5 minutes in a single block), the gradual, trial-by-trial development of motor adaptation might have been cut short by the end of the experimental blocks. That is, the observed between-condition differences might simply reflect differences in the time needed for the development of the motor adjustments at different delays. At longer delays, force optimization could still be possible, but it might require more, or longer exposures to the given action–effect conjunction than at short delays, for which an action–effect binding is

established quickly. The gradual development of force optimization at 400-ms delay within the (ca. 9 minutes long) adaptation block of Experiment 3 clearly supports this idea.

The results also allow one to speculate that *fast optimization* observed with immediate effects and short delays (requiring only a few trials) and *slow optimization* with longer delays (possibly requiring hundreds or thousands of trials) are qualitatively different processes. While the slowly developing force optimization might reflect a strategic process relying on understanding the causal connection between the action and its delayed effect, fast adjustments could point to a process automatically integrating the motor and sensory components of the action. Indeed, models with two adaptive processes working on different timescales have been suggested for explaining various motor adaptation phenomena (Shadmehr, Smith, & Krakauer, 2010).

Besides indicating the possibility for slow optimization at longer delays, the results of Experiment 3 might also provide further insight into the mechanisms of motor optimization with delayed effects. Surprisingly, this experiment showed that exposure to action–effect conjunctions with long delay (400 ms) between them results subsequently in a more efficient force optimization in an intermediate delay condition (200-ms action–effect delay), than extended practice with immediate auditory effects. Explaining this result is not trivial, but the results of the explorative analyses might allow some speculations. The continuous force adaptation through the entire 400-ms delay adaptation block, and the absence of similar adaptation in the 0-ms delay block may signal that the processes driving adaptation were not operating with similar intensity in the two groups. One may speculate that participants already in the process of integrating the action and the delayed effect have an advantage over those who—in the absence of such a delayed effect—were not engaged in a similar integration attempt. The nature of the integration process is unclear. One possibility is that the process is that of temporal recalibration (Stetson et al., 2006). The recalibration hypothesis posits that

immediacy has a distinguished position in the temporal relation of action and its consequences. In the case of delayed sensory effects, the cognitive system strives to restore the perceived synchronicity of the action and the elicited stimulus (or-in case of longer delays—to approach synchronicity as much as possible). This recalibration could either mean a perceptual compression of the action–effect interval (Haggard, Clark, & Kalogeras, 2002), a perceptual forward shift of the events following the action (Stetson et al., 2006), or an updating of the probabilistic distribution of the expected action-effects (Cao et al., 2017). In these terms, participants who were adapted to a 400-ms action-effect interval, had to recalibrate the temporal representation of the two events, resulting in the perceived length of the delay becoming shorter than the actual interval between the motor and sensory events. For the group adapted to 0-ms delay, however, no recalibration was necessary. As shown by the action-effect reversal phenomenon (Stetson et al., 2006; Timm, Schönwiesner, SanMiguel, & Schröger, 2014), in extreme cases, recalibration can result in events that are consequences of the actions being perceived as happening before the actions. Thus, it can be argued that as a result of recalibration, participants who were adapted to 400-ms delays perceived the 200-ms delay in the test condition as shorter, whereas participants adapted to immediate effects had a more "realistic" temporal representation of the action-effect delay. The applied force in the test condition (200-ms delay) might reflect how participants perceived the length of the action-effect interval: Weaker force (i.e., more efficient optimization) in the 400-ms adapted group might indicate that this group perceived the delay as being shorter than participants adapted to immediate effects.

The recalibration hypothesis provides an interpretation that fits well with studies about various aspects of delayed action-effects. However, an explanation based on different modes of action control for short and long delays might be also plausible. As suggested before, the lack of automatic action–effect binding at long delays might result in participants utilizing

similar action control mechanisms and strategies, as in the case of actions without auditory effects, but possibly also control processes relying on a different (non-automatic) type of action—effect association, which could be reflected in the slow optimization observed in the 400-ms delay adaptation block. It seems plausible to suggest, that in the adaptation phase the group adapted to 400-ms delay had to utilize these control mechanisms to a larger extent, than participants adapted to 0-ms delay, who could effectively control actions by relying mainly on auditory feedback and automatic action—effect binding. This might have provided the former group with an advantage at intermediate delays, as they were able to draw on a larger variety of control strategies, while the group who only experienced immediate effects was only experienced in the use of control processes which rely on automatic action—effect integration (which would be less effective in the 200-ms delay condition , as indicated by Experiment 1 and 2), resulting in a more pronounced force optimization for the 400-ms delay adapted participants in the test condition (200-ms delay).

Conclusion

The present study shows that action-effect-related motor adaptation depends on action–sound delay: Auditory stimuli can be used as feedback for action control more effectively if they follow the motor act within a short period. The critical delay is about 200 ms: In this delay range a fast optimization of action force is possible. However, even within this time-window, the efficiency of the optimization is affected by prior experience with action–sound delay. Exploratory results also indicate that even with auditory effects outside the 200-ms limit, action-effect-related motor adaptation is possible, but requires more or longer experience with the action–effect delay.

These results implicate that contingency-information provided by action-effects occurring after a critical point are not readily utilized for adjusting and planning subsequent

movements. Despite the obvious causal connection between the two events, the information flow between the motor and sensory systems seems to be limited in certain cases. Thus, it seems that action-effect-related motor adaptation is not simply the result of some rational strategic process, but also might require a form of automatic binding between action and effect that is different from the links required for other types of sensory–motor interactions and for establishing causal relationships between the two events.

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Tables

Table 1.

Pairwise comparison (Wilcoxon signed-rank tests, with Holm correction) of the six conditions with different action-effect delays in Experiment 1.

Condition/ Action-effect	0 ms	200 ms	400 ms	800 ms	1600 ms
delay	0 1115	200 1115		000 1115	1000 1115
200 ms	5^{***}				
200 IIIS	(.975)		-	-	-
400 mg	0^{***}	84^*			
400 IIIS	(1.0)	(.586)	-	-	-
800 ms	0^{***}	97	184		
	(1.0)	(.522)	(.094)	-	-
1600 mg	0^{***}	30***	90	138	
1000 ms	(1.0)	(.852)	(.557)	(.320)	-
	0^{***}	43***	89	102	161
motor	(1.0)	(.788)	(.562)	(.498)	(.207)

*note: For the Wilcoxon signed-rank tests T-values are displayed (with the r rank biserial correlation coefficient in parentheses). Significance values: p < .05, **p < .01, ***p < .001

five conditions with different delion-effect delays in Experiment 2.								
Action–effect delay/Condition	0 ms	50 ms	100 ms	200 ms				
50 ms	54 ^{**} (.7014)	-	-	-				
100 ms	30 ^{***} (.841)	115 (.392)	-	-				
200 ms	1 ^{****} (.995)	26 ^{***} (.862)	6 ^{***} (.968)	-				
motor	0 ^{****} (1.0)	0 ^{***} (1.0)	3 ^{***} (.984)	14 ^{***} (.926)				

Table 2.

Pairwise comparison (Wilcoxon signed-rank tests, with Holm correction) of the five conditions with different action–effect delays in Experiment 2.

*note: For the Wilcoxon signed-rank tests *T*-values are displayed (with the *r* rank biserial correlation coefficient in parentheses). Significance values: p < .05, **p < .01, ***p < .001

	motor		adaptation		test		control	
Group	М	SD	М	SD	М	SD	М	SD
0-ms delay-	(no tone)		(0-ms delay)		(200-ms delay)		(400-ms delay)	
adapted	3.403	0.580	2.869	0.549	2.999	0.253	3.018	0.247
400-ms	(no t	cone)	(400-m	s delay)	(200-m	s delay)	(0-ms	delay)
delay-adapted	3.436	0.525	2.851	0.365	2.882	0.337	2.948	0.297

Table 3.Between-action intervals for the two groups in the four conditions ofExperiment 3.

*note: The delay values in parentheses above the mean and SD values display the action–effect delays for the groups in the given condition.



Figure 1. Experimental blocks completed by the participants in the experimental session that

included Experiment 1.



Figure 2. Histograms of between-action intervals in the six conditions of Experiment 1. (All registered actions of all participants. There were a few instances in all conditions when actions were registered immediately after another action, however according to epoch-rejection criteria, these actions were not included in the analyses.)



Figure 3. Left: Tukey plots displaying the distribution of the individual applied force in the different conditions in Experiment 1. (Horizontal lines display the median of the group, upper

and lower hinges of the box the 1^{st} and 3^{rd} quartiles, whiskers cover datapoints within the 1.5 interquartile range below and above the 1^{st} and 3^{rd} quartiles respectively, and points represent values that fall outside the range covered by the whiskers.) Right: Temporal force profiles of all pinches of a representative participant in the six conditions.



Figure 4. Experimental blocks completed by the participants in the experimental session that included Experiment 1.



Figure 5. Histograms of between-action intervals in the five conditions of Experiment 2. (All registered actions of all participants included in the final sample.)



Figure 6. Left: Tukey plots displaying the distribution of the individual applied force in the different conditions in Experiment 2. Right: FSR force profiles of all pinches of a representative participant in the five conditions (Experiment 2).



Figure 7. Tukey plots showing the distribution of individual pinch force values in the four conditions of Experiment 3. Data of the two groups are displayed separately, the 0-ms delay-

adapted group with orange (white), the 400-ms delay-adapted group with green (grey) color. Action–effect delays for the two groups in each condition are displayed next to the whiskers of the boxplot.



Figure 8. Tukey plots showing the distribution of individual pinch force values in the first (trials: 1-60), second (trials: 61-120) and third (trials: 121-180) part of the adaptation block in

Experiment 3. Data of the two groups are displayed separately, the group adapted to 0-ms delays with orange (white), the group adapted to 400-ms delays with green (grey) color.

Supplementary material for

Temporal constraints in the use of auditory action-effects for motor optimization

Bence Neszmélyi, János Horváth

1. Exploratory analyses of trial-by-trial motor adaptation

Neszmélyi and Horváth (2017) suggested that the difference in force between actions with and without distinctive auditory effects might be the result of trial-by-trial force optimization in conditions in which actions elicited a sound. That is, during the first trials of a block, if the applied force is sufficiently strong to elicit a sound, participants apply a reduced pinch force in the subsequent trial. Although the present experiments were not designed with the goal to analyze such tendencies, exploratory analyses were conducted on the data of Experiment 3 to assess such within-block changes in action force.

Analysis of within-block force optimization tendencies is not reported for Experiment 1 and 2. Results of Experiment 3 indicated that action-effect-related motor adaptation at a certain action–effect delay might be affected by prior exposure to different delays (see Main text: Experiment 3, Results). In Experiment 3, participants of a given group performed the experimental blocks in the same order, thus—at any point in the experiment—optimization performance of each participant was affected by the same experience. Therefore, variability within a given group only represents differences in the individual responses to identical circumstances. As Experiment 1 and 2 were designed to examine action-effect-related motor adaptation in a within-participant design (in contrast to the between-participant design of Experiment 3), block order was randomized in these studies to eliminate block-order effects.

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On one hand, this increased the validity of comparing action forces in a blocked manner. On the other hand, however, as prior experience of participants differed when encountering a certain action–effect delay, variance in trial-by-trial optimization reflects not only individual variance in the ability of using tones with a given delay for controlling actions, but also a variability in prior experience. As these factors cannot be separated in a group-level visualization and analysis of the data, interpretation of within block tendencies would not be straightforward in these experiments.

In Experiment 3, the distribution of individual forces in each group was plotted trialto-trial for each block (Figure S1-S4). These plots suggested that the development of the optimization process was different in the two groups. To statistically explore these tendencies (post-hoc), each block was divided into three parts (1st, 2nd and 3rd part, Figure S5), and the median force was calculated for each participant in each condition and part. The within-group force differences between parts were examined by Friedman's tests in each group and block (with pairwise Wilcoxon signed-rank tests used for follow-up analysis), while between-group differences were assessed by submitting force values to Wicoxon rank-sum tests. Effect sizes were estimated by calculating the rank biserial correlation coefficient (King, Rosopa, & Minium, 2011; Kerby, 2014).

The visual inspection of Figure S1 suggests similar tendencies in the two groups in the motor condition: a gradual, slow increase in force. The Friedman's test comparing the block parts (see Figure S5, top, left), however, was only significant for the 0-ms delay-adapted group ($\chi^2(2) = 13.857$, p < .001). Follow-up analyses revealed that for this group the applied force in the first part differed significantly from those in the second (T = 10, p = .005, r = .810) and third (T = 3, p < .001, r = .943) block parts. No significant between-group difference was found in any of the block parts.

The analysis of the adaptation block is described in the main text. (See Figure S2 for trial-by-trial distribution of individual pinch force values in this condition.)

The visual inspection of Figure S3 suggests that in the test block (200-ms delay for both groups), the 400-ms delay-adapted group optimized the force level trial-by-trial during the first ca. 20 trials, whereas for participants adapted to 0-ms delays no trial-by-trial optimization is apparent. The Friedman's tests, however, did not show significant differences between block parts for either group (see Figure S5, bottom, left) which may suggest that if there was indeed a stepwise optimization in the 400-ms delay-adapted group at the beginning of the block, then this occurred more rapidly than the resolution of the measurement interval (i.e., the aggregation over 20 actions) allowed. The force differences between the groups were significant for all three block parts (1^{st} : U = 41, p = .014, r = .549; 2^{nd} : U = 33, p = .004, r = .637; 3^{rd} : U = 39, p = .011, r = .571).

For the analysis of the control block the same principles apply as for the analyses reported in the main text: Between-group differences cannot be unequivocally interpreted, because there was more than one factor (action–effect delay in the block and prior experience) that might have affected performance of the two groups differently. In the control block, pinch-forces of the 400-ms delay-adapted group seem consistent during the block (in this condition eliciting tones with 0-ms delay), whereas the 0-ms delay-adapted group (in this condition eliciting tones with 400-ms action–effect delay) seems to gradually reduce pinch forces in the first part of the experiment (Figure S4). Confirming this observation, Friedman's test comparing action forces in the block parts (Figure S5, bottom, right) was only significant in the 0-ms delay-adapted group ($\chi^2(2) = 10.429$, p = .005). The follow-up analysis indicated that in this group the applied force was stronger in the first part than in the second (T = 18, p = .030, r = .657) and third (T = 3, p < .001, r = .943) parts. The applied force was significantly stronger in the 0-ms delay-adapted group than in the 400-ms delay adapted group in all three

block-parts (1st: U = 5, p < 0.001, r = .945; 2nd: U = 13, p < 0.001, r = .857; 3rd: U = 21, p < 0.001, r = .769).

2. Online and offline factors in action-effect-related motor adaptation

Previous studies usually regarded tone eliciting actions like button pressing or tapping as ballistic (Chase, Harvey, Standfast, Rapin, & Sutton, 1961; Chase, Rapin, Gilden, Sutton, & Guilfoyle, 1961; Finney & Warren, 2002; Karlovich & Graham, 1966, 1967; Neszmélyi & Horváth, 2017). That is, it was assumed that movement execution is predetermined, and online movement adjustments in response to sensory events occurring during the movement do not play a substantial role. Action-effect-related motor adaptation was also observed with such ballistic action types (i.e., tapping on a table, or pressing a button: Horváth, Bíró & Neszmélyi, in press), suggesting that—at least in those cases—the phenomenon reflects action planning processes. Although for such movements-executed in a timeframe below 60 msthe involvement of online motor-adjustments is clearly unrealistic, for pinching-based on the latency of the force peaks (Table S1)—one could still argue that the effects reported in the present study could reflect online control processes and not differences in action planning. Indeed, the assumption that participants increase pressure on the device until they perceive the elicited tone, would provide a plausible explanation for the observed delay-dependent effects. Tone onset would signal that the force-threshold was exceeded, and—in response participants could initiate a pinch-release. Longer action-effect delays would provide an extended time frame for increasing pressure on the device, which could explain higher peak forces in these conditions.

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Experiment	1		Experimen	Experiment 2			
Blocks/	Median	IQR (ms)	Blocks/	Median	IQR (ms)		
Action-	peak		Action-	peak			
effect	latency		effect	latency			
delay	(ms)		delay	(ms)			
0-ms	91	31	0-ms	84	33		
200-ms	170	136	50-ms	106	65		
400-ms	170	116	100-ms	122	63		
800-ms	161	93	200-ms	148	68		
1600-ms	185	110	Motor	192	70		
Motor	196	131					

Table S1.Signal peak latencies in Experiment 1 and 2

*note: For the estimation of the inter quartile range (IQR) the method recommended by Hyndman and Fan (1996) was applied.

A closer inspection of the force signals, however, makes this explanation unlikely. If action execution is indeed determined by online mechanisms, force peaks should unequivocally signal a time-point when these control processes are already at work. (Although considering the interplay of flexor and extensor muscles in determining the dynamics of the actions, a reaction to tone onset has to start several milliseconds before the force signal peak.) Two temporal limits might be considered for actions being affected by online control processes: It is *physically* impossible that online control mechanisms could affect actions, if the force signal peaks before the tone presentation. However, considering human reaction times to sensory stimuli, it is also *physiologically* implausible that actions would be affected by online processes in the first 60 ms after tone presentation—even considering that reaction times might be enhanced by a startle response (Carlsen, Dakin, Chua, & Franks, 2007; Valls-Solé, Rothwell, Goulart, Cossu, & Munoz, 1999; Valls-Solé, Solé, Valldeoriola, Munoz, Gonzalez, & Tolosa, 1995), or the fact that reactions are faster for movement adjustments, than for starting a motor response (Gritsenko, Yakovenko, & Kalaska, 2009; Haith, Pakpoor, & Krakauer, 2016). Thus, if the force signal peaks before tone

delay + 60 ms, potential contributions of online control mechanisms can be excluded with high certainty. Given the force peak latencies in Experiment 1 and 2 (Table S1), online control mechanisms may only contribute to 0 and 50-ms delay conditions. (Presuming more realistic reaction times, it seems unlikely that online processes play a substantial role even in the 50-ms delay condition.)

However, it still could be argued that adaptation with short (100, 200 ms) action– effect delays reflects offline optimization, while the immediate condition (and maybe the 50ms delay condition) is dominated by online mechanisms. (As action-effect-related motor adaptation was also observed when immediate auditory effects were elicited by button presses, or by tapping on the table—in which cases online control is unlikely—this online effect would be specific both in regard to temporal properties of action execution and to length of action–effect delay.)

To address this issue, for Experiment 1 and 2, pairwise comparisons reported in the main text were repeated, but instead of using force maxima to characterize actions, a measure that should exclusively reflect motor planning (offline) processes was applied¹. Because online mechanisms are unlikely to contribute the movement in the first 60-ms following tone onset, we characterized each action by its impulse (integral of the force signal) in the 10–60-ms interval. (Between the actions, participants held the response device between their fingers, resulting in a small, below-threshold force being applied to the FSR, even when actions were not produced. The first 10 ms of the registered actions was discarded when determining the force impulse, so that the measure would not be affected by this "baseline" force level, and the calculated values would reflect the dynamics of the individual actions.) As for the force

¹ The analyses using the impulse (force integrated over time) measure are only reported in the Supplementary material. Although impulse is a useful measure in the present study because it allows the characterization of the ballistic part of the actions, in general, peak force (which is widely used in the literature) may be a better option for the characterization of actions, because the force peak corresponds to the point of maximal tactile feedback (Kunde, Koch, & Hoffman, 2004), therefore it may be a distinguished point (or even a goal) of the interaction.

peaks, for each participant, in each condition, the median impulse in the given condition was calculated, and between-condition differences were explored by pairwise Wilcoxon signed-rank tests (with Holm correction). The results (shown in Table S2 and S3, and in Figure S6) are very similar to those observed when characterizing actions with force maxima. Importantly, the impulse was significantly smaller in the 0-ms delay condition than in the motor condition in both experiments, which shows that these motor differences were caused by processes related to action planning².

Table S2.

Pairwise comparison (Wilcoxon signed-rank tests, with Holm correction) of the six conditions in Experiment 1 using the force integral in the 10—60-ms interval

mervai					
Condition/ Action–effect delay	0 ms	200 ms	400 ms	800 ms	1600 ms
200 ms	44 ^{**} (.783)		-	-	-
400 ms	44 ^{**} (.783)	174 (.143)	-	-	-
800 ms	22 ^{***} (.892)	147 (.276)	105 (.483)	-	_
1600 ms	46 ^{**} (.774)	189 (.069)	137 (.325)	157 (.227)	-
motor	37 ^{***} (.818)	136 (.330)	85 (.581)	181 (.108)	135 (.335)

*note: For the Wilcoxon signed-rank tests *T*-values are displayed (with the *r* rank biserial correlation coefficient in parentheses).

Significance values: p < .05, p < .01, p < .01

² Although with the force impulse measure in the 10–60-ms interval no significant effect was found in the first experiment for the 200-ms delay condition, an optimization effect was also present in this condition, when using the 150—200-ms interval for calculating the force impulse (T = 85, p = .042, r = .581). This time window can still not be affected by online reaction to the auditory action-effect, when the auditory stimuli are presented with a 200-ms delay

Table S3.

Action–effect delay/Condition	0 ms	50 ms	100 ms	200 ms
50 ms	72 [*] (.619)	-	-	-
100 ms	74 [*] (.608)	155 (.180)	-	-
200 ms	27 ^{***} (.857)	103 (.455)	94 (.503)	-
motor	3 ^{***} (.984)	6 ^{***} (.968)	9 ^{***} (.952)	39 ^{***} (.794)

Pairwise comparison (Wilcoxon signed-rank tests, with Holm correction) of the five conditions in Experiment 2 using the force integral in the 10–60-ms interval

*note: For the Wilcoxon signed-rank tests *T*-values are displayed (with the *r* rank biserial correlation coefficient in parentheses). Significance values: p < .05, **p < .01, ***p < .001

3. Carry-over effects for Experiment 1 and 2

As described in the main text, Experiment 1 and Experiment 2 were preceded by experiments which examined processes of action-effect-related motor adaptation in a between-group arrangement (see Figure 1 and 4 in the main text; Experiment 2 was preceded by the experiment reported as Experiment 3 in the current study; the experiment that was completed before Experiment 1 is not reported in this study.) Although a short break and additional training blocks were inserted between experiments, it is possible that carry-over effects influenced the results of Experiment 1 and 2. To test this, in both experiments, participants were divided into two groups, according to their group assignments in the preceding experiments. Pinch forces were compared between groups

across all blocks, and all force-analyses reported in the main text were performed separately for the groups.

Before Experiment 1 an experiment was conducted, which half of the participants (group A; N = 14, age: 19–24, female: 12, right handed: 13) started with two consecutive motor blocks (no tone elicited by the actions), and then concluded with two blocks in which FSR-pinches elicited immediate auditory effects (pure tone, with the same acoustic features as in Experiment 1). The other group (group B; N = 14, age: 18–24, female: 14, right handed: 14) performed motor and immediate auditory effect conditions (also two consecutive blocks of each block type) in reverse order (see Figure 1 in the main text). In Experiment 1, no carry-over effects could be observed. There was no significant difference between the two groups in any of the six action–effect delay conditions. Also, the pattern of delay-effects was very similar in the both groups to that reported in the main text for the whole sample (Table S4, Figure S7). Although the 200-ms delay condition was not significant in group A, this can be attributed to reduced sample size, as even in this group, significance (with Holm correction) very closely approached the significance limit (p = 0.067) and effect sizes in the two groups were very similar.

Table S4.

Action– effect delay/ Condition	0	ms	200	ms	400 ms		800 ms		1600ms	
	Group A	Group B	Group A	Group B	Group A	Group B	Group A	Group B	Group A	Group B
200 ms	0 ^{**} (1.0)	2 ^{**} (.962)		-		-		-		-
400 ms	0 ^{**} (1.0)	0 ^{**} (1.0)	20 (.619)	24 (.543)	-	-		-		-
800 ms	0 ^{**} (1.0)	0 ^{**} (1.0)	21 (.600)	28 (.467)	50 (.048)	44 (.162)		-		-
1600 ms	0 ^{**} (1.0)	0 ^{**} (1.0)	11 (.790)	3 ^{**} (.943)	34 (.352)	18 (.657)	44 (.162)	32 (.390)		-
motor	0 ^{**} (1.0)	0 ^{**} (1.0)	11 (.790)	9* (.829)	28 (.467)	19 (.638)	24 (.543)	27 (.486)	47 (.105)	37 (.295)

Pairwise comparison (Wilcoxon signed-rank tests, with Holm correction) of the six conditions in Experiment 1 performed separately for the two groups

*note: For the Wilcoxon signed-rank tests *T*-values are displayed (with the *r* rank biserial correlation coefficient in parentheses).

Significance values: p < .05, p < .01, p < .001

In Experiment 2, the results show that a carry-over effect from Experiment 3 persisted, as force-optimization for all delays (except for the motor condition) was significantly more pronounced for the group adapted to 400-ms delays in Experiment 3 (0ms delay: U = 38, p = .009, r = .582; 50-ms delay: U = 50, p = .048, r = .451; 100-ms delay: U = 32, p = .003, r = .648; 200-ms delay: U = 49, p = .043, r = .462). Importantly, however, the delay effects observed in Experiment 2 were still observable separately in both groups (Table S4, Figure S8).

Table S5.

Action–effect delay/Condition	0 1	ms	50	ms	100 ms		200 ms		
	Adapted to 0-ms delay	Adapted to 400- ms delay							
50 ms	15 [*] (.714)	14 (.692)		-		-		-	
100 ms	9* (.829)	6 [*] (.868)	38 (.276)	23 (.495)		-		-	
200 ms	0 ^{**} (1.0)	1 ^{**} (.978)	11 [*] (.790)	4 ^{**} (.912)	1 ^{**} (.981)	2 ^{**} (.956)		-	
motor	0 ^{**} (1.0)	0 ^{**} (1.0)	0 ^{**} (1.0)	0 ^{**} (1.0)	1 ^{**} (.981)	1 ^{**} (.978)	5 ^{**} (.905)	3 ^{**} (.934)	

Pairwise comparison (Wilcoxon signed-rank tests, with Holm correction) of the five conditions in Experiment 2 performed separately for the two groups

*note: For the Wilcoxon signed-rank tests *T*-values are displayed (with the *r* rank biserial correlation coefficient in parentheses). Significance values: p < .05, p < .01, p < .001

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Figure S1. Tukey-plots showing the distributions of individual pinch force values trial-by-trial in the motor block of Experiment 3. Data of the two groups are displayed separately, the group adapted to 0-ms delays with orange, the group adapted to 400-ms delays with green color. (Horizontal lines display the median of the group, upper and lower hinges of the box the 1st and 3rd quartiles, whiskers cover datapoints within the 1.5 interquartile range below and above the 1st and 3rd quartiles respectively, and points represent values that fall outside the range covered by the whiskers.)



Figure S2. Tukey-plots showing the distributions of individual pinch force values trial-by-trial in the adaptation block of Experiment 3.



Figure S3. Tukey-plots showing the distributions of individual pinch force values trial-by-trial in the test block of Experiment 3.


Figure S4. Tukey-plots showing the distributions of individual pinch force values trial-by-trial in the control block of Experiment 3.



Figure S5. Tukey-plots of individual pinch force distributions in the first, second and third part of each block in Experiment 3.



Figure S6. Tukey-plots of individual impulse distributions in the conditions of Experiment 1 (left) and 2 (right), calculated by integrating force values in the 10-60-ms time window.



Figure S7. Tukey-plots of individual pinch force distributions in the six conditions of Experiment 1, for participants assigned to Group A (who started with actions that did not produce auditory effects) and Group B (who started with actions that produced immediate auditory effects) in the preceding experiment (not reported in the current study).



Figure S8. Tukey-plots of individual pinch force distributions in the five conditions of Experiment 2, for participants assigned to the 0-ms and 400-ms delay adapted group in the preceding Experiment 3.