CITATION

Perceptual Surprise Aides Inhibitory Motor Control

Jan R. Wessel
University of Iowa and University of Iowa Hospitals and Clinics

Neurophysiological studies of cortico-motor excitability have shown that unexpected sounds are followed by motor inhibition. In a recent study, Leiva, Parmentier, Elchlepp, and Verbruggen (2015) derived a prediction from these findings: unexpected, task-irrelevant sounds should increase the ability to withhold motor responses in a Go/NoGo task. Contrary to that prediction, they found that playing unexpected sounds before NoGo-stimuli decreased the likelihood of successful motor inhibition. However, we here argue that the relative timing of unexpected events relative to NoGo-related motor activity is key. Cortico-motor inhibition can be found only until ~150 ms after the onset of unexpected sounds. Therefore, since Leiva et al. (2015) placed their sounds 200 ms prior to NoGo-stimuli, the inhibitory influence of unexpected sounds may have fully abated before the critical inhibitory period. Consequently, we here repeated their study, with 1 key change: task-irrelevant sounds were presented 50 ms after NoGo-stimulus onset, which ensures that cortico-motor inhibition takes place when motor inhibition is needed. Across 4 experiments, this changed timing produced the results predicted by the previous cortico-motor suppression findings: More responses were successfully withheld after unexpected sounds. These data provide new evidence for the fact that unexpected events can engage an inhibitory control process and benefit motor inhibition.

Public Significance Statement
Recent neurophysiological studies have shown that unexpected events elicit activity in brain networks associated with the stopping of action and broadly suppress the excitability of the motor system. This implies the possibility that when humans rapidly have to stop an action, the occurrence of an unexpected event may help them do so. Across 4 experiments, we find that when unexpected sounds are played shortly (50 ms) after the onset of a stimulus that requires the stopping of a prepotent motor response, human participants are indeed better at stopping their actions. This points toward a crucial interaction between action stopping and surprise processing in humans, suggesting that motor inhibition and attentional processing are tightly linked.

Keywords: motor inhibition, surprise, novelty, unexpected events, attention

The occurrence of unexpected, surprising perceptual events has well-characterized effects on behavior. One of the most ubiquitous findings is that slower motor RTs (reaction time [RT]) are observed after unexpected perceptual events (Dawson, Schell, Beers, & Kelly, 1982; Parmentier, Elford, Escera, Andres, & San Miguel, 2008). These effects can be observed regardless of response modality (Berti & Schroger, 2004; Wessel & Aron, 2013) or the sensory modality of the unexpected event (Ljungberg & Parmentier, 2012; Parmentier, Ljungberg, Elsley, & Lindkvist, 2011). This slowing of motor emission could be the result of an inhibitory control mechanism: in a study that used transcranial magnetic stimulation to probe the corticospinal excitability of the motor system (Wessel & Aron, 2013), we found that unexpected sounds were followed by nonselective suppression of motor excitability: At 150 ms following the onset of an unexpected sound, motor excitability within task-unrelated hand muscles was suppressed. This was interpreted as the result of a fronto-basal ganglia brain network for motor inhibition (Aron, Robbins, & Poldrack, 2014; Jahanshahi, Obeso, Rothwell, & Obeso, 2015; Kenemans, 2015), which is known to be involved in cancelling responses in motor inhibition tasks like the stop-signal task (Logan & Cowan, 1984). This brain network is known to nonselectively suppress motor excitability when rapidly recruited (Badry et al., 2009; Wessel, Reynoso, & Aron, 2013). In line with the purported recruitment of this brain network after unexpected perceptual events, its neural signature on the scalp was found to be active following surprising sounds (Wessel & Aron, 2013), strengthening the theoretical link between surprise and motor inhibition. Based on these results, we proposed a model according to which motor (and potentially...
cognitive) activity is momentarily inhibited after unexpected events, which would then aid and enable the subsequent shifting of attention toward the source of the surprise (Wessel & Aron, 2013, 2017).

In a recent observation published in this journal, Leiva and colleagues tested a prediction of this theory (Leiva, Parmentier, Elchlepp, & Verbruggen, 2015). The authors investigated whether task-irrelevant unexpected sounds presented during a two-choice Go/NoGo task would be beneficial to motor inhibition. Specifically, they presented task-irrelevant sounds before each Go and NoGo-stimulus. On a subset of trials, the sounds were unexpected: instead of the standard 600 Hz sine-wave tone, an environmental sound was played. Based on our theory, Leiva, et al. (2015) predicted that if surprise did in fact induce motor inhibition, unexpected sounds should lead to a greater probability of successfully withholding the response to the NoGo-stimulus. They found the opposite pattern: after unexpected compared to expected sounds, fewer responses were successfully withheld.

However, the experimental design in that study may have been suboptimal when taking into account the timing of motor inhibition associated with unexpected events. Specifically, in our original study (Wessel & Aron, 2013), we found that corticospinal excitability was suppressed—that is, motor activity was inhibited—at 150 ms following the onset of an unexpected sound, but not beyond that (we also tested cortico-motor effects at 175 ms or 200 ms after unexpected sounds, but found no difference to expected sounds). In the Leiva et al. (2015) study, sounds began 200 ms before the Go/NoGo stimulus. Hence, the inhibitory influence of the unexpected event had likely already ended before the imperative stimulus was even presented—and therefore, before any motor inhibition was necessary.

Therefore, we here repeated Experiment 1 in Leiva et al. (2015), with one key difference: Expected and unexpected task-irrelevant sounds were presented with an onset at 50 ms after the display of the imperative Go or NoGo-stimulus (instead of 200 ms before it). We predicted that this timing would trigger surprise-related inhibitory activity at 200 ms following the onset of the Go/NoGo stimulus (50 ms + 150 ms, in accordance with the timing of cortico-motor suppression in Wessel & Aron, 2013), and consequently lead to more successful motor inhibition after unexpected sounds.

**Experiment 1**

**Method**

**Participants.** Twenty (15 female) undergraduate students at the University of Iowa (mean age: 18.65, SD = 3.9) participated in exchange for course credit. This was the same number of participants as in Leiva et al. (2015). Participants signed written informed consent and the experiments were approved by the University of Iowa Institutional Review Board (#201510772).

**Apparatus and stimuli.** Stimuli were presented on a Dell Optiplex 7800 computer connected to a 21-inch Dell flatscreen using Psychtoolbox 3 (Brainard, 1997) running in MATLAB (TheMathWorks, Natick, MA) under Fedora Linux. Responses were made using a standard QWERTY keyboard.

**Experimental paradigm.** The experiment aimed to closely emulate Experiment 1 in Leiva et al. (2015). In short, the imperative Go/NoGo stimuli were white letters W and M (.8 cm × .8 cm) which appeared against a black background, 3 cm to the left or right of a central fixation cross. The Go/NoGo mapping to the two letters was counterbalanced. Participants responded to the stimuli by pressing the “q” or “p” keys on the keyboard using their left or right index fingers, depending on which side the stimulus was presented.

Each trial began with a fixation cross (300 ms), which was followed by the Go/NoGo stimulus 50 ms after the Go/NoGo stimulus, a sound was played. The standard sound was a 200 ms sine-wave sound at 600 Hz and occurred on 80% of trials, and the unexpected sounds (20% of trials) were the same birdsong segments used in Wessel and Aron (2013). These were 90 samples taken from European Starling songbirds (courtesy of Jordan A. Comins), which were matched in amplitude envelope to the standard sine wave tone. One third of the trials were NoGo-trials, and two thirds were Go trials. Participants were instructed that the sound would be irrelevant to their response (Go or NoGo). Similar to Leiva et al. (2015), we used an adaptive deadline procedure: After three correct responses, the deadline was adjusted downward by 50 ms, and after each miss it was adjusted by 50 ms in the opposite direction. Leiva et al. (2015) did not report their starting point for the deadline, so we set this to 500 ms (note that our deadline procedure differed from Leiva et al. (2015) in another way, see Experiment 4). After each trial, participants received feedback (“correct” on correct Go responses, “incorrect” on incorrect Go responses, “too slow” when responses were made outside of the response deadline, “do not respond” on NoGo trials with responses, and “correct” on NoGo trials on which the response was successfully withheld). The feedback was displayed for 1,000 ms. As in Leiva et al. (2015), participants performed 15 blocks of 60 trials. In our experiment, the first block consisted of training, and did not include unexpected sounds. That block was excluded from further analysis. At the end of each block, we displayed the same feedback as Leiva et al. (2015) (mean RT, number of incorrect responses and misses, percentage of successfully withheld responses). Participants had to pause 15 s before they could proceed to the next block.

In total, there were four changes from the original Leiva et al. (2015) experiment:

1. The onset of the sound was 50 ms post-Go or NoGo-stimulus, instead of 200 ms prior to the stimulus.
2. The first block of trials was used as practice, did not include unexpected sounds, and was excluded from the final analysis.
4. In Leiva et al. (2015) participants had an extraordinarily high miss rate, owing to the very strict response deadline (see previous paragraph). In their experiment, the authors did not record responses made after the deadline (Fabrice Parmentier, personal communication, September 5th, 2016). Importantly, this was the case on both Go and NoGo trials. Therefore, some “successful” NoGo trials
may have included a response, yet after the deadline. Hence, we made sure to record responses even after the deadline. We will report the results both in the way Leiva et al. (2015) reported them (i.e., all trials with responses after the deadline counted as “no response was made”), and also with the trials with postdeadline responses counted as “response was made.”

Analyses. Analyses were performed in MATLAB (TheMathWorks, Natick, MA). Paired samples t tests were used to test the main hypothesis. All analysis scripts are available at www2.psychology.uiowa.edu/faculty/wessel/Leiva.zip.

Results

Descriptive statistics are in Table 1. Miss rates were comparable with Leiva et al. (2015), owing to the strict response deadline. If misses were defined as the complete absence of responses (i.e., no response was made after the deadline), this number was much lower (M = 2.32% for unexpected and 1.25% for expected sounds). As in Leiva et al. (2015), Go-trial RT (GoRT) was slower on trials with unexpected sounds, t(19) = 2.49, p = .02, Cohen’s d = 0.22, in line with previous literature. Crucially, unlike in Leiva et al. (2015) and as predicted, the probability of responding on a NoGo-trial was significantly lower on trials with unexpected compared with trials with expected sounds, t(19) = 4.83, p = .0001, Cohen’s d = .68. This finding had a medium-to-large effect size (according to Cohen’s guidelines for d), and was numerically present in 17 out of the 20 participants (Figure 1, left panel). Furthermore, if the successful NoGo-trials that included responses after the deadline were excluded, this pattern remained identical (mean p(respnogo) = .27 for unexpected sounds and .38 for expected sounds; t(19) = 4.93, p = .00009, Cohen’s d = .66). The raw data underlying these results can be found alongside the analysis scripts at www2.psychology.uiowa.edu/faculty/wessel/Leiva.zip.

Discussion

When unexpected sounds are presented at a time during which their hypothesized inhibitory effects overlap with the initiation of the motor response, they do lead to more effective motor inhibition/response prevention.

In Experiment 2, we aimed to replicate the finding from Experiment 1, as well as the finding from Leiva et al. (2015) using our stimulus material. To this end, we reran Experiment 1, except now we randomly varied sound-timings: half of the sounds were presented at 200 ms before stimulus onset, and the other half at 50 ms following stimulus onset (as in Experiment 1).

Experiment 2

Method

Participants. Twenty (12 female) undergraduate students at the University of Iowa (mean age: 18.69, SD = 4.1) participated in exchange for course credit. Participants signed written informed consent and the experiments were approved by the University of Iowa Institutional Review Board (#201510772).

Apparatus and stimuli. Same as in Experiment 1.

Experimental paradigm. Same as in Experiment 1, but instead of all sounds being presented at 50 ms after stimulus-onset, the onset of the sound on each trial varied randomly between 200-ms prestimulus onset and 50-ms poststimulus onset.

Analyses. Same as Experiment 1. Additionally, repeated-measures ANOVAs (Timing × Expectancy) and follow-up paired samples t tests were used to test the influence of the different time points on the surprise-related influence on NoGo-inhibition.

Results

Descriptive results can be found in Table 2. With regards to GoRT, rmANOVA revealed main effects of both timing, F(1/19) = 74.24, p = 5.5 × 10^-08, partial-η^2 = 0.8; and expectancy, F(1/19) = 13.78, p = .0015, partial-η^2 = 0.42, with a significant interaction, F(1/79) = 11.06, p = .004, partial-η^2 = 0.37. Follow-up t tests show that under both timing conditions, Go-trial RTs were slowed for unexpected compared to expected sounds (−200 ms timing: t(19) = 1.93, p = .068, d = 0.2; +50 ms timing: t(19) = 5.12, p = 6.04 × 10^-05, d = 0.36). With regards to the main hypothesis test, rmANOVA revealed main effects of both timing, F(1/19) = 91.29, p = 1.1 × 10^-08, partial-η^2 = 0.83; and expectancy, F(1/19) = 8.76, p = .008, partial-η^2 = 0.32, on the probability of responding on NoGo-trials, as well as a marginally significant interaction, F(1/79) = 3.45, p = .079, partial-η^2 = 0.15. Follow-up t tests revealed that under both timing conditions, the probability of responding to a NoGo-stimulus was decreased following unexpected sounds (Figure 1, middle panel); however, this effect only reached significance in the + 50 ms timing condition (−200ms timing: t(19) = 0.74, p = .47, d = 0.14; +50 ms timing: t(19) = 5.02, p = 7.68 × 10^-05, d = 0.92). These results remained qualitatively identical if responses after the deadline were excluded from the analyses.

Discussion

We replicated the finding from Experiment 1, namely, that unexpected sounds presented 50 ms after stimulus-onset lead to a lower chance of responding to a NoGo-stimulus. However, we did not find that sounds presented 200 ms before stimulus onset lead to a decrement in NoGo-inhibition (the finding reported by Leiva et al., 2015). This clearly shows that the effect of unexpected sounds depends on the timing of the stimuli. Notably, we found elongated response times for unexpected events under both timing conditions, showing that unexpected events had effects on behav-

Table 1

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Unexpected tone</th>
<th>Expected tone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>p (correct)</td>
<td>.99</td>
<td>.01</td>
</tr>
<tr>
<td>p (miss)</td>
<td>.256</td>
<td>.056</td>
</tr>
<tr>
<td>RT</td>
<td>452</td>
<td>45</td>
</tr>
<tr>
<td>p (respnogo)</td>
<td>.231</td>
<td>.144</td>
</tr>
</tbody>
</table>

Note. RT = reaction time; M = mean; SD = standard deviation. Same measures as in Leiva et al. (2015) Experiment 1.
ior across time points, which are consistent with both Leiva et al. (2015) and Experiment 1 above.

In Experiment 3, we made further attempts to replicate the exact conditions of Leiva et al. (2015) as closely possible to see whether the beneficial effects of unexpected events on NoGo-inhibition at +50-ms poststimulus would replicate under their exact conditions. To this end, we reached out to the authors of the Leiva et al. (2015) study and received their stimulus material (Verbruggen, Parmentier, Leiva; personal communication, February 7th, 2017). We furthermore used the instruction slides that were provided for download along the original article. Then, we reran Experiment 2 with the new stimulus material. Prior to data collection, we performed a power analysis using GPower 3 (Faul, Erdfelder, Lang, & Buchner, 2007). We calculated the estimated effect size from the Leiva et al. (2015) study (dz = .588) according to the formula provided by Lakens (Equation 7; Lakens, 2013), and ensured to collect the necessary sample size to produce a two-sided power of .8 for a paired sample t test (N = 25).

**Experiment 3**

**Method**

**Participants.** Twenty-six (18 female) undergraduate students at the University of Iowa (mean age: 18.75, SD = 3.69) participated in exchange for course credit. Participants signed written informed consent and the experiments were approved by the University of Iowa Institutional Review Board (#201510772).

**Apparatus and stimuli.** Same as in Experiment 1, except that the sounds were exchanged with the expected and unexpected sounds used by Leiva et al. (2015).

**Experimental paradigm.** Same as in Experiment 2.

**Analyses.** Same as in Experiment 2.

**Results**

Descriptive results can be found in Table 3. With regards to GoRT, rmANOVA revealed main effects of both timing, F(1/25) = 113.89, p = 8.5 × 10^{-11}, partial-η² = 0.82; and expectancy, F(1/25) = 10.73, p = .003, partial-η² = 0.3, with no interaction, F(1/103) = 1.6, p = .22, partial-η² = 0.06. Individual t tests show that under both timing conditions, Go-trial RTs were slowed for unexpected compared to expected sounds; however, this was only significant for the +50 ms condition (+200 ms timing: t(25) = 1.65, p = .11, d = 0.15, d = 0.21; +50 ms timing: t(25) = 3.02, p = .006, d = 0.3). With regards to the main hypothesis test, rmANOVA revealed main effects of both timing, F(1/25) = 65.99, p = 1.7 × 10^{-10}, partial-η² = 0.73, and expectancy, F(1/25) = 14.89, p = .0007, partial-η² = 0.37, on the probability of responding on NoGo-trials, as well as a significant interaction, F(1/103) = 6.85, p = .015, partial-η² = 0.22. Follow-up t tests reveal that under both timing conditions, the probability of responding to a

<table>
<thead>
<tr>
<th>Table 2 Behavioral Results by Sound-Timing (+200 ms vs. +50 ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dependent variable</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>p (correct)</td>
</tr>
<tr>
<td>p (miss)</td>
</tr>
<tr>
<td>RT</td>
</tr>
<tr>
<td>p (respnogo)</td>
</tr>
</tbody>
</table>

*Note.* RT = reaction time; M = mean; SD = standard deviation. Same measures as in Leiva et al. (2015) Experiment 1.
NoGo-stimulus was decreased following unexpected sounds (Figure 1, right panel); however, this effect only reached significance in the +50 ms timing condition (−200 ms timing: t(25) = 6, p = .55, d = 0.99; +50 ms timing: t(25) = 5.7599, p = 5.2975e-06, d = 1.1843, d = 0.92). These results remained qualitatively identical if responses after the deadline were excluded from the analyses.

Discussion

The results from Experiment 3 were qualitatively identical to Experiment 2. NoGo-inhibition was aided by unexpected tones at 50-ms poststimulus. Sounds at 200-ms prestimulus had no effect on motor inhibition. That leaves the question as to why we could not reproduce the inhibitory decrement in the −200 ms condition tested by Leiva et al. (2015) in either experiment. One notable observation is that GoRT in our experiment was slower in the 200 ms condition compared with Leiva et al.’s (2015) original study (406 ms/400 ms for unexpected/expected events, respectively, vs. 318 ms/313 ms in Leiva et al., 2015). Hence, after obtaining the original MATLAB code from the Leiva et al. (2015) experiment (Vebruggen & Parmentier, February 7th, 2017; personal communication), we compared the exact implementation of the RT deadline tracking procedure with our experiments. This comparison showed that there was a slight difference in the exact implementation of the deadline procedure—while we interpreted the deadline procedure as described in the article as “The deadline decreases if last three trials were correct go-trials,” Leiva et al. (2015) actually implemented their criterion as “The deadline decreases if last three go-trials were correct.” The latter is an easier criterion to satisfy, and therefore leads to a more readily decreasing deadline, producing faster RTs overall. Hence, we reran Experiment 3, but this time, we implemented the deadline procedure exactly as in Leiva et al. (2015).

Experiment 4

Method

Participants. Twenty (10 female) undergraduate students at the University of Iowa (mean age: 19.4, SD = 1.31) participated in exchange for course credit. Participants signed written informed consent and the experiments were approved by the University of Iowa Institutional Review Board (#201510772). One participant was replaced because they pressed the wrong button throughout the experiment.

Apparatus and stimuli. Same as in Experiment 3.

Experimental paradigm. Same as in Experiment 3, except with the exact deadline tracking procedure used by Leiva et al. (2015).

Analyses. Same as in Experiment 3.

Results

Descriptive results can be found in Table 4. With regards to GoRT, rmANOVA revealed main effects of both timing, F(1/19) = 146.86, p = 2.19 * 10−10; partial-\eta² = 0.89; and expectancy, F(1/19) = 24.84, p = 8.23 * 10−05, partial-\eta² = 0.57, with a significant interaction, F(1/19) = 9.3, p = .007, partial-\eta² = 0.33. Follow-up t tests show that under both timing conditions, Go-trial RTs were slowed for unexpected compared to expected sounds (−200 ms timing: t(19) = 1.9, p = .073, d = 0.18; +50 ms

Table 4

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>−200 ms</th>
<th></th>
<th></th>
<th>+50 ms</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unexpected tone</td>
<td></td>
<td></td>
<td>Expected tone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p (correct)</td>
<td>.94</td>
<td>.06</td>
<td>.93</td>
<td>.05</td>
<td>1.00</td>
<td>.01</td>
</tr>
<tr>
<td>p (miss)</td>
<td>.30</td>
<td>.05</td>
<td>.25</td>
<td>.04</td>
<td>.488</td>
<td>.09</td>
</tr>
<tr>
<td>RT</td>
<td>277</td>
<td>34</td>
<td>272</td>
<td>30</td>
<td>323</td>
<td>38</td>
</tr>
<tr>
<td>p (resporgo)</td>
<td>.515</td>
<td>.13</td>
<td>.515</td>
<td>.18</td>
<td>.187</td>
<td>.127</td>
</tr>
</tbody>
</table>

Note. RT = reaction time; M = mean; SD = standard deviation. Same measures as in Leiva et al. (2015) Experiment 1.
follow-up unexpected sounds in the ability of responding to a NoGo-stimulus was decreased following inhibitory deficit found by Leiva et al. (2015) in the no difference. It is still unclear why we cannot find the predicted unexpected sounds, whereas in the were identical to Experiments 3 and 4: In the producing RT levels comparable with Leiva et al. (2015). With discussion interaction, probability of responding on NoGo-trials, as well as a significant F(2) = 2.06, p = 10^-08, partial-\eta^2 = 0.82; and expectancy, F(1/19) = 16.96, p = 0.0006, partial-\eta^2 = 0.47, on the probability of responding on NoGo-trials, as well as a significant interaction, F(1/19) = 21.91, p = .0002, partial-\eta^2 = 0.54. Follow-up t tests reveal that as in previous experiments, the probability of responding to a NoGo-stimulus was decreased following unexpected sounds in the +50 ms timing condition, t(19) = -5.45, p = 2.93 * 10^-05, d = 1.21. In the -200 ms condition, however, the two condition means were virtually identical (-200 ms timing condition, t(19) = 0.06, p = .95, d = 0.008; +50 ms timing). These results remained qualitatively identical if responses after the deadline were excluded from the analyses.

Discussion

Our alteration of the deadline procedure proved effective in producing RT levels comparable with Leiva et al. (2015). With respect to motor inhibition, however, the results of Experiment 4 were identical to Experiments 3 and 4: In the +50 ms timing condition, there was a clear inhibitory benefit associated with unexpected sounds, whereas in the -200 ms condition, there was no difference. It is still unclear why we cannot find the predicted inhibitory deficit found by Leiva et al. (2015) in the -200 ms condition. Given that Experiment 4 was virtually identical to Experiment 1 in Leiva et al. (2015) (which we verified by running their code on our computers and comparing it to our experiment), and given that both conditions produce measurable effects on RT (showing RT slowing after unexpected tones for both the +50 ms and the -200 ms condition, as in Leiva et al., 2015), we hypothesize that the only factor that could account for the difference is that the effects found by Leiva et al. (2015) for the 200-ms prestimulus time point may be moderated by the presence of sounds with different timing—that is, the fact that we used both -200 ms and +50 ms as onset conditions in our experiment. Notably, the inhibitory benefit we found for the +50 ms time point does not seem subject to the same moderator, as it is significant in our Experiments 1 (no interleaving of timings), 2 (interleaved timing), 3 (interleaved timing), and 4 (interleaved timing).

Combined Sample Analysis

To provide a CI for the effect size of the inhibitory benefit in the +50 ms timing condition, we pooled participants from all four experiments (see Figure 2). In the resulting sample of N = 86, the effect of unexpected tones on motor inhibition was significant, t(85) = 10.2, p = 2.27 * 10^-16, with an effect size of d = .81. The 95% CI for this effect size was [.49, 1.11]. Conversely, the combined sample of 66 participants from Experiments 2–4, who also performed the -200 ms condition, revealed a nonsignificant effect of unexpected events at that timing, t(65) = .83, p = .41, with an effect size of d = .06 (95% CI [-.41, .28]). Given the effect size estimate from Leiva et al. (2015) for that condition (dz = .588), we achieved a post hoc power of 99.7% for a two-sided difference at an alpha level of p < .05. To further quantify the evidence for either outcome, we performed a Bayes factor analysis. At the most common prior scaling (t = sqrt(2)/2), the Bayes factor for the difference in inhibitory success between unexpected and expected trials in the -200 ms condition was 4.16 (“barely worth mentioning,” i.e., the lowest category of evidence according to Jeffreys, 1998). In contrast the evidence for a difference between the event types at +50 ms was 3.91 * 10^13, representing “decisive evidence” according to Jeffreys (the cut-off for “decisive” evidence is 100).

General Discussion

Across four experiments, we found that unexpected sounds can indeed benefit motor inhibition. This is in contrast to the previous study of Leiva et al. (2015), which used the same experimental design, yet with a different timing between the NoGo-stimulus and

Figure 2. Combined behavioral results from all four experiments. The y-axis shows the probability of responding on a NoGo-stimulus. Gray circles denote individual subjects’ data within each condition, with paired data connected by gray lines. Black horizontal lines denote the mean, whereas the errors bars denote 1 standard error of the mean.
the onset of the task-irrelevant sounds. In our experiment, unexpected sounds that started at 50 ms following a NoGo stimulus clearly increased the likelihood of successful motor inhibition (compared to expected sounds). These results proved to be highly reliable across all four samples, with an overall effect size of $d = .8$ (95% CI [.49, −1.11]) across all 86 participants, and 75 participants numerically showing the effect in the predicted direction (87.2%). The results from Experiments 2 through 4 furthermore show that the inhibitory benefit of unexpected perceptual events clearly depends on the relative timing of the unexpected event vis-à-vis the NoGo-stimulus, in line with predictions made based on physiological measures of cortico-motor excitability. Taken together, our findings are further evidence for the theory that unexpected perceptual events induce motor inhibition, which can be observed for about 150 ms after the unexpected event (Wessel & Aron, 2013, 2017).

Notably, Leiva et al. (2015) included a second experiment in their original study. We would argue that the results from that experiment are in line with our findings and wider theory. Unlike in their Experiment 1 (the subject of the current study), sounds were task-relevant in that second experiment. However, only a subset of trials included sounds. The sounds were presented at the same time as the Go signal, and functioned as the NoGo signal. In that experimental design, the likelihood of successfully withholding the response was indeed increased when sounds were unexpected. However, because Leiva et al. (2015) had already ruled out the possibility that unexpected events increased the likelihood of successful motor inhibition based on the findings from their first experiment, they used the second experiment to test an independent hypothesis—namely, whether unexpected sounds would “lead to the automatic execution of a prepotent response on no-go trials” (p. 1200). Yet in light of our current results, which show that unexpected events at 50-ms poststimulus can in fact aid inhibition, the results of Experiment 2 in Leiva et al. (2015) can also be interpreted as an inhibitory benefit of the unexpected event. Because the unexpected sounds were presented at the same time as the Go-signal, surprise-related motor inhibition may have aided at inhibiting the response on NoGo-trials, similar to our 50-ms post-stimulus timing.

Importantly, while the study of Leiva et al. (2015) and the current experiment show opposite results at first glance, both results are informative in regard to the cascade of processing after unexpected events. While our study showed that unexpected events can benefit inhibitory control if their occurrence is temporally aligned with the motor activity that is to be inhibited, Leiva et al.’s (2015) study shows that this beneficial effect does not sustain beyond a certain time period (similar to what we find in the 200 ms condition). Leiva et al.’s (2015) results also suggest that the effect actually reverses if the imperative stimulus occurs after an unexpected event (even though this could not be replicated in our current experiments). The fact that the inhibitory motor activity triggered by unexpected events is highly temporally specific and transient is in line with our initial study, which showed that cortico-motor excitability is no longer suppressed at time points beyond 150-ms postunexpected event. In that study (Wessel & Aron, 2013), we proposed a cascade of processing after unexpected events, in which the recognition of an unexpected event—which can happen as early as 50 ms after stimulus onset in the auditory domain (Gamble & Woldorff, 2015)—is followed by a quick inhibitory process, which is then followed by attentional reorienting. This argument was made based on the relative timing of the different signatures that represent motor inhibition (suppression of corticospinal excitability at 150 ms) and attentional reorienting (the fronto-central novelty-P3 event-related potential, which started after the initial inhibition reflected in the suppressed corticomotor excitability; Wessel & Aron, 2013).

We have further explicated this theory in a more recent study (Wessel et al., 2016), which could explain why unexpected events may potentially have an adverse effect on inhibition when presented at the 200-ms prestimulus time point used by Leiva et al. (2015). In that study, we found that the inhibitory effect of unexpected perceptual events may not be constrained to the motor system. From prior behavioral findings, it was already well-known that unexpected perceptual events can have adverse effects on cognitive processing that is not primarily motor (e.g., Schroger, 1996). We found that such cognitive effects of unexpected events (in our example, unexpected sounds during the maintenance interval in a verbal working memory task) are mediated by inhibitory activity of the same brain mechanism that inhibits the motor system (Wessel et al., 2016). Specifically, unexpected sounds that interrupted working memory maintenance were accompanied by stronger activations in the brain circuitry underlying inhibitory control. We concluded that some types of cognitive representations (such as verbal working memory) are also subject to inhibition mediated by the brain circuitry underlying action stopping. Based on these results, we proposed that unexpected events recruit the inhibitory brain mechanism to momentarily inhibit both cognitive and motor representations. This would allow the cognitive system to momentarily disengage from ongoing motor and cognitive processes, thereby enabling it to switch attention to the unexpected event. We believe that this is an adaptive mechanism aimed at allowing a more effective, rapid processing of unexpected events (Wessel & Aron, 2017). However, it would lead to an impairment if a task is to be performed in the time period during which the attentional focus has shifted onto the unexpected event, and away from the primary task (similar to an attentional blink, see below). We believe that the current results, combined with the findings from Leiva et al. (2015) are in line with that proposed sequence of processes: unexpected events initially have a beneficial effect on motor inhibition, as long as the motor activity to be inhibited overlaps with the time period that immediately follows the onset of the unexpected event (up to ~150 ms). This initial benefit can then potentially turn into a decrement if an important event is presented while attentional focus has disengaged from the primary task (i.e., in time periods later than 150 ms after the unexpected event, as was the case in Leiva et al., 2015).

Notably, the chronological sequence proposed here is also in line with the theory of the attentional blink, that is, the inability to perceive a second salient target event after the presentation of a first salient event (Arnell & Jolicoeur, 1999; Raymond, Shapiro, & Arnell, 1992). Such studies usually find that the attentional blink begins at around 180 ms following the first salient event, and lasts for around 300 ms (Raymond et al., 1992). Hence, the attentional blink begins immediately after the end of the cortico-motor suppression (150 ms). Our theory, as well as the theory of the attentional blink, would predict that perfor-
formance should return to baseline after the interference produced by the unexpected event (or the attentional blink) is over (Wessel, 2016; Wessel & Aron, 2017). In other words, no difference should be found between unexpected and expected events after the initial inhibitory benefit (observed in the current study) and the subsequent attentional blink have worn off. This theory is easily testable using the experimental framework developed by Leiva et al. (2015).

Questions that remain to be answered pertain the boundary conditions under which the effects reported by Leiva et al. (2015) occur. This is especially important because we could not replicate their findings in our interleaved-timing design in the current study. In addition to the interleaved timing, one potential moderator is the volume of the tones. While the sounds were presented at conversational volume in our current study (to stay in line with our previous studies), it has been shown that tones that are loud enough to evoke a startle response can speed up motor processing (Valls-Sole et al., 1995). While this is unlikely to explain the divergent results between our study and the study undertaken by Leiva et al. (2015) (because GoRTs were slower following unexpected sounds in both studies), a systematic investigation of startle and startle-responses on motor activity may reveal different effects on motor inhibition. Furthermore, it would be informative to delineate the nature of which types of unexpected events can facilitate motor inhibition. For example, it remains to be seen whether there is an inhibitory benefit when surprise is produced by the unexpected absence of an event (instead of the unexpected alteration of an event).

Taken together, the authors of Leiva et al. (2015) derived an interesting hypothesis from our (Wessel & Aron, 2013) and other (Corbetta & Shulman, 2002) theories of distraction after unexpected events, namely, that unexpected perceptual events could benefit motor inhibition. They developed a novel and highly adaptable experimental paradigm, which could allow a detailed testing of the exact timeline of the interaction between inhibitory control, surprise processing, and attentional orienting. Our slight variation of the relative stimulus timing of the paradigm in the current study clearly shows that under circumstances predicted by our theory, unexpected perceptual events can indeed benefit inhibitory control.

References


Received September 29, 2016
Revision received April 24, 2017
Accepted April 25, 2017

SURPRISE AIDS MOTOR INHIBITION