Startle Reduces Recall of a Recently Learned Internal Model

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Abstract — Recent work has shown that preplanned motor programs are released early from subcortical areas by the using a startling acoustic stimulus (SAS). Our question is whether this response might also contain a recently learned internal model, which draws on experience to predict and compensate for expected perturbations in a feedforward manner. Studies of adaptation to robotic forces have shown some evidence of this, but were potentially confounded by cocontraction caused by startle. We performed a new adaptation experiment using a visually distorted field that could not be confounded by cocontraction. We found that in all subjects that exhibited startle, the startle stimulus (1) reduced performance of the recently learned task (2) reduced after-effect magnitudes. Because startle reduced but did not eliminate the recall of learned control, we suggest that multiple neural centers (cortical and subcortical) are involved in such learning and adaptation, which can impact training areas such as piloting, teleoperation, sports, and rehabilitation.

Keywords- adaptation; learning; startle; movement; dynamics; reaching; arm; upper extremity; healthy;

I. INTRODUCTION

Due to physiological constraints (proprioceptive and visual), humans cannot execute relatively fast and smoothly coordinated arm movements without specific neural mechanisms that plan a movement prior to its release. Thus, the central nervous system compiles a model of the action that estimates the motor commands needed to carry out the movement. This is referred to as the feedforward mode of motor control, whereby an internal model is constantly modified and acquired through motor learning [1].

The application of unexpected perturbations, either kinematic (i.e. visual distortions) or dynamic (i.e. applied force fields) have been experimentally useful in understanding the adaptation and learning responses of the feedforward motor program [2, 3, 4, 5]. A typical adaptation experiment tests these concepts by exposing subjects to a perturbation. After a long training phase, the subjects eventually learn to move in the presence of the perturbation and begin to move in a straight line as they would if undisturbed [2]. When unexpectedly turned off and people return to the “normal” world, they make errors in their movements, called after-effects that are nearly symmetrical to the initial errors that occur when the subjects are first exposed [2]. Such after-effects reveal the learned forward model that predicts the dynamics of the movement before it even begins.

In another line of research it has recently been shown that the planning of a movement can be probed with a startling acoustic stimulus (SAS). During simple reaction time tasks, the presentation of SAS up to 1400 ms prior to, or coincident with the imperative “go” cue (GO) to initiate movement results in the imperative, rapid release of the planned movement with onset times typically 80ms earlier than voluntary movements [6, 7]. Moreover, the spatial and temporal characteristics of the movement sequence remain intact. Based on the early latency of the onset of movement, it has been proposed that SAS releases a pre-planned “motor program” from subcortical structures and occurs if the task is known before initial movement takes place [8]. This result is quite dramatic in programmed stepping response actions, where the SAS triggers not only an earlier release of movement (sometimes premature to the “go” signal), but a more and more complete feedforward control program (involving appropriate preparatory weight shifting) as the time of the SAS stimulus timing approached the GO cue [3]. Movement preparation evidently involves a progressive buildup of a feedforward motor program over time before the go signal.

These findings are consistent with the feedforward mode of neural control whereby the motor sequence is prepared before voluntary movement. However, in a previous paper we provided evidence that suggests that the intended motor sequence fails to remain intact when released by startle following the unexpected removal of a force field after adaptive training [9]. The reduction in the size of after-effects indicates that the recently learned internal model is disrupted by SAS. Despite the influence of SAS on feedforward control
resulting from adaptation, the magnitude of the released internal model did not progressively increase as the timing of SAS approached the GO cue, which would be consistent with the build-up and readiness of the feedforward program.

Due to drastic changes in the EMG profiles resulting from SAS, there is concern that the reduction in after-effects was a result of the co-contraction of muscles rather than a disruption in learning. In force-field adaptation, it has been shown that co-contraction can be a means to reduce movement error [10]. However, this technique cannot be utilized when adapting to a perturbation that requires a different hand path, such as adaptation to a visual rotated environment. Thus, this study describes the use of healthy subjects executing reaching movements using a robotic apparatus capable of distorting the visual field to test the hypothesis that SAS disrupts the release of movement trajectory consistent with the after-effects of adaptive training. Such disruption should reduce the size of after-effects, revealing that SAS disrupts learning.

II. Procedure

A. Apparatus

The experiment used a planar haptics and graphics robotic system called the manipulandum, described previously [11, 12]. While sitting in front of the robot and holding the robotic arm end effector, subjects are able to execute two-degree of freedom movements (Fig. 1). The robot includes a projected overlay display of visual cues relevant to the experimental task and real-time visual feedback of the end-effector position recorded by digital encoders.

An analog tone (1000 Hz, 40ms, <1ms rise time) produced by a function generator was used to create an auditory startle stimulus. The tone was amplified to produce a stimulus with an intensity of 124 dB, which was measured using a digital sound level meter (Model 407730, Extech Instruments Corp, MA). The auditory startle stimulus was presented to the subject via a marine horn (M58H - 30 Watt Horn Speaker; MG Electronics, NY) placed 30 cm directly behind the subjects head. A real-time control system developed using MathWorks XPCTarget allowed for precise timing of the SAS output.

Surface EMG recordings were implemented to assess reaction times and startle responses, described previously [13]. Surface EMG recordings were collected from the following superficial muscles: anterior deltoid, posterior deltoid, long head triceps brachii, biceps brachii, and right sternocleistomastoid (SCM) using a Bagnoli EMG System. Data was digitally sampled at 1 kHz (National Instruments USB-6229) and continuously collected using a customized program in Labview. Post-processing of raw EMG data included removal of bias, full-wave rectification and low-pass filtering (cutoff 25 Hz) using a 5th order zero-lag Butterworth filter.

B. Protocol

Eleven healthy adult right-handed subjects free from neurological or musculoskeletal disorders and naive to the learning paradigms participated in this study. Subjects grasped the handle of the robot and performed a series of reaching movements in the outward direction to a blue (radius = 18mm) visual target located 15cm from a fixed start position, indicated by an “x” on the screen. Real-time visual feedback of the handle position was displayed on the screen as a green cursor. Chair height was adjusted so that movements departed from a center point located in the horizontal plane, 30 cm below the chin (approximately standard table height) and 20 cm anterior to the chin.

Each trial consisted of the appearance of a blue target followed by a low-level acoustic stimulus (83dB) after a fixed time period of 2.5s to indicate the GO cue. Subjects were instructed to release their movement in response to the GO cue as early as possible and to execute the movement to the target as accurate as possible. Moving the cursor within the target and holding it for 500ms resulted in a change in the target’s color, denoting the end of the movement. Subjects were then instructed to move the handle back to the start position, at which time the target changed back to the original color, indicating the start of a new trial.

The numerical value of velocity-based movement onset time was displayed on the screen at the end of each movement to encourage subjects to decrease their response time to the GO cue. Movement onset was defined as the time the handle velocity reached a threshold of 0.1m/s relative to the time of the GO cue.

Change in target color was used to provide feedback on movement time, defined as the amount of time that elapsed between movement onset and when the target was reached. The target turned green if the movement time was within a predefined range of 450-700 ms, consistent with typical movement times seen for 15 cm movements [1]. In addition, the word “Speed”, displayed in the top left-hand corner of the workspace, turned green if the peak speed of the movement was within a predefined range of 0.7-1.1 m/s, consistent with movement speeds for discrete movements. We controlled for movement time and speed to avoid trials where subjects possibly engaged in a technique to reduce speed in order to...
increase accuracy [14]. Failure to execute the movement within the respective ranges of either of these kinematic features resulted in a change in color of the visual feedback to red..

Each subject participated in an experiment that has the following phases:

1. **Familiarization**: To become familiar with the experimental conditions, subjects made 30 movements to the target. These movements allowed subjects to arrive at a full understanding of the task, to become comfortable and well seated at the apparatus and learn to accurately perform movements along the intended straight line trajectory.

2. **Baseline**: Subjects performed five movements which were used to establish a baseline pattern before prolonged training began. Based on our experience, five movements were sufficient to test for statistical stability of their movement pattern.

3. **Initial Exposure**: In a subset of 40 movements in all, on randomly selected trials, (one in every 8 movements) subjects were exposed to a distortion of the visual feedback of the handle position. This visual distortion (VD) was arranged by rotating the visual field by an angle of 45 degrees from the start position. Consequently, any movement of the robot handle directed away from the start position resulted in a deviation of the cursor at a 45 degree angle. 8 subjects received a clockwise (CW) rotation, whereas 3 subjects received a counterclockwise (CCW) rotation.

   In addition, on randomly selected trials, (one in every 8 movements) subjects were exposed to SAS at one of 3 startle timing conditions (500, 250 or 0ms prior to the GO). These trials were used to evaluate the effects of startle on their performance to move within the null field prior to training.

4. **Training**: A total of 100 movements were performed in all, where subjects consistently trained in the presence of the visually rotated field.

5. **Evaluation**: 160 movements were performed with visual distortion, but now several randomly selected trials (one in every 8 movements) evaluated the effects of learning and how it is modulated by SAS. In these trials, subjects experienced either the unexpected removal of VD or the unexpected removal of VD with an SAS (occurring at -500, -250 and -0 ms prior to the “go” signal).

   **C. Analysis**

Angular deviation from an ideal straight line movement to the target was the primary measure of movement error, since the after-effects of adaptation, seen when the CW (CCW) visual rotation is unexpectedly removed, are a CCW (CW) bend of the movement path. Initial direction error is defined as the angle between the ideal straight line movement to the target and the vector formed from the point of velocity-based movement onset to 150ms along the path of the trajectory. The velocity-based movement onset was determined when the handle velocity reached 0.1 m/s.

Surface EMG recordings were used to assess movement release times. EMG-based movement onset is defined as the point at which initial agonist muscle (anterior deltoid) activity sustained a rise above baseline levels (two standard deviations above the average resting activity) for 25ms. All EMG onsets were measured relative to stimulus onset (i.e. startle stimulus for SAS trials and GO stimulus for non startle trials). Due to the strictness of this algorithm, it was often necessary to visually locate and manually adjust the onset mark to the point at which activity first increases.

An early burst in neck muscle activity (SCM), with a subsequent short latency release time has been shown to be the most reliable indicator of a startle reaction [13]. However, during normal reaching movements, neck muscles are sometimes inherently active to stabilize the head. To distinguish from other SCM activity, SCM onset within the time window of 30-100ms was used to determine if SCM activity was related to startle [11]. EMG based movement onsets relative to the stimulus onset were considered to be early if they were more than one standard deviation from the mean movement onsets of control non-startle trials (last 25 trials in training phase). All SAS catch trials that exhibited startle related SCM activity with an accompanying early release of movement (ERM) were considered a startle response and separated for analysis.

SAS catch trials and their angular deviation from an ideal straight line in both groups were compared to non-startle catch trials using a paired t-test. Differences with a p-value less than 0.05 were considered significant. One-Way ANOVA with Tukey’s HSD post hoc comparisons was used to determine if the three SAS cases are statistically different than the non-startle case (α=0.05).

III. RESULTS

We first examined the influence of startle on each subject and separated, from the dataset, the SAS catch trials that exhibited a startle response as described above. It was quite evident that some subjects were more vulnerable to the startle stimulus than others. The yield in the number of startle responses detected was comparatively lower than most startle studies [13]. Of the eleven subjects only four showed a sustained startle response (52 out of 60 SAS catch trials), complete with a burst in SCM activity and an ERM. Three subjects did not exhibit any startle response and 5 subjects displayed a startle related early release of movement without accompanying SCM. Habituation to the startle stimulus or the lack of buildup of the motor program and readiness to perform the task are possible explanations for the deficit of startle responses seen in subjects [13].

EMG-based movement onset times for the SAS catch trials of the four subjects that exhibited a sustained startle response were compared to non startle control trials from the end of training. The mean and standard deviation for control trials and for SAS trials was 143.57ms (+45.07ms) and 84.83ms (+23.30ms), respectively. Differences across conditions are shown in Fig. 2 using a wings plot showing the means and 95% confidence interval of movement errors for each subject.
A paired t-test revealed that when a startle response was detected, movement was released significantly earlier (~58ms) than voluntary responses; t(3) = 7.64 p = .0047.

As in other experiments of this type, baseline trajectories approximated straight lines (Fig. 3A), initial exposure to visual distortion resulted in a deviation in the CW (CCW) direction (Fig. 3B), motions again approximated straight lines by the end of training (Fig 3C), and trajectories were distorted in the CCW (CW) direction in the catch trials where the visually distorted field was unexpectedly removed, revealing after-effects of adaptation (Fig. 3D).

Similar patterns in the after-effects were also visible when SAS was presented. Fig. 3D gives a visual of one subject’s after-effect trajectories for when SAS was not present (black) and when SAS was administered at one of the three different time points (-500, -250, -0ms) relative to the GO cue (green, blue, red, respectively) causing an early release of movement and SCM response. The dots represent the position along the path where movement error is measured. Angles between the baseline trajectory and the after-effect trajectories were smaller in the SAS situation. Although the patterns of the trajectories for the after-effects were similar for when SAS was present or absent, the magnitude of the after-effects for both cases were compared.

The group results point to similar trends (Fig 4). The mean of movement errors for the non startle case was calculated to be 33.78 degrees, with a standard error of ±6.97. The means of movement errors for when SAS was administered at -500ms, -250ms and 0ms was calculated to be 14.84 degrees, 18.80 degrees and 18.03 degrees, respectively, with standard errors of ±7.20, ±8.63 and ±7.29, respectively. Differences across condition are shown in Fig. 4 using a wings plot showing the means and 95% confidence interval of movement errors for each subject for each condition. One-way Repeated Measures ANOVA revealed a main effect of task condition F(3,12) = 23.265, p =.0001. Post hoc analysis using Tukey’s HSD showed that movement error for the three startle timing conditions were significantly different than the non-startle condition, but did not differ significantly between SAS timing conditions. These results are similar to those previously documented where after-effect catch trials were a result of adaptation to a force field [9].

Despite the low yield in number of SAS trials that exhibited a startle response, another group of subjects (5 subjects) showed to have a consistent early release of movement, but without the accompanying SCM. Consistent with other studies, it is possible that these subjects were less affected by startle, but had at least some response related to startle that lead to an accelerated response [7, 13]. We compared the movement errors of this startle response group (SCM-/ERM+) to non startle catch trials. We found that, in the presence of SAS, after-effects were significantly reduced from Non SAS catch trials when SAS caused an ERM without SCM activity. However, the reduction was less drastic than the startle response group where SCM was present (SCM+/ERM+). Differences across groups are shown in Fig. 5 using a wings plot (one subject had a cross between the two startle response groups – indicated in red). Since the timing of SAS did not have an effect on the magnitude of after-effects, all the SAS timing conditions in both groups were combined and each subject’s data is normalized to the average movement error of their respective non-SAS catch trials. A paired t-test indicated
that the magnitude of after-effects for both groups are significantly lower than the non-startle catch trials (SCM+/ERM+ $t(3) = 7.219$ $p = .0055$; SCM-/ERM+ $t(4) = 3.4525$ $p = .0260$). The evidence suggests that SAS causes a degradation of the movement trajectories consistent with after-effects, but the degree of such reduction may depend on the type of startle response.

It is clear that SAS has the effect of degrading after-effects associated with catch trials, but these results do not answer a potentially lingering question of whether SAS has a similar effect on performance (i.e. startle while training within a perturbed field). To explore the effect of startle on performance, on a separate set of subjects (7 in total), we tested a similar paradigm that now included intermittent randomly placed trials with the presence of VD and SAS in the evaluation phase in addition to the already existing Non SAS and SAS catch trials. The trials of interest were those that either posed as a catch trial (i.e. the removal of VD or the removal of VD with SAS @ -250, 0ms) or a performance trial (i.e. presence of VD with SAS @ -250, 0ms). We hypothesized that SAS would have a similar effect in that it would degrade performance of a newly learned internal model, thus causing an increase in movement error.

Apart from the Non SAS catch trials, the dataset only evaluated SAS trials in which SCM activity was present and an ERM was calculated. Also, the two SAS timing conditions were combined for both SAS catch trials and SAS performance trials. We compared the SAS catch trials to SAS performance trials by normalizing to the mean of the Non SAS catch trials and the mean of the last five trials of the training phase, respectively.

We found that SAS, not only reduces after-effects associated with the removal of VD, but also reduces performance while moving within a visually distorted field, causing an increase in movement error. Fig. 6 shows a wings plot giving a visual on the reduction of movement error in SAS catch trials (left) and a reduction in performance of SAS performance trials (right). A paired t-test indicated that the magnitude of after-effects for SAS catch trials are significantly smaller than the Non SAS catch trials; $t(6) = 3.8563$ $p = .0084$. Also, a paired t-test indicated that the magnitude of movement errors for SAS performance trials were significantly lower than the performance at the end of training; $t(6) = 2.90$ $p = .0273$.

![Figure 4. Movement errors in the after effects catch trials (where VD is unexpectedly turned off) for the cases of no startle and startle at several delays (horizontal axis), compared to baseline error. Statistical comparison of groups using Tukey post-hoc tests revealed significant differences between non startle and each of the three startle conditions (shown by black lines connecting brackets at the top). Hence, SAS significantly reduced but did not eliminate nor did it reverse the error seen in the after-effects trials.](image4)

![Figure 5. Movement errors in SAS catch trials normalized to mean Non SAS catch trials for both startle response groups (horizontal axis). Group means are considered significantly different than non-SAS means if the upper bound of the groups 95% confidence interval (shaded diamond areas) is less than 1. Hence, SAS significantly reduced after-effects in both startle response groups.](image5)

![Figure 6. Movement errors in SAS catch trials and SAS performance trials normalized to mean non-SAS catch trials and mean end of training performance, respectively. Group means are considered significantly different if the upper bound of the group 95% confidence interval is less than 1. Hence, SAS significantly reduced after-effects in catch trials and reduced performance.](image6)
IV. DISCUSSION

This paper presented results where subjects learned how to operate a machine in the presence of the challenging rotation of the visual feedback. We found that in all subjects that exhibited startle, the startle stimulus (1) reduced performance of the learned task (2) reduced after-effect magnitudes. This study was an important step to understanding both startle and its relationship to recall of feedforward control. In contrast to adaptation to force fields, startling a person who has adapted to a visually distorted field cannot be confounded by the effects of cocontraction, since cocontraction would not cause after-effects to be diminished.

To the best of our knowledge, these results are the first to probe the effects of startle framed in the context of robot and sensory adaptation. Because the underlying startle mechanisms are believed to originate in the brainstem and other subcortical regions, and because startle reduced but did not eliminate the recall of learned control, we suggest that multiple neural centers (cortical and subcortical) are involved in such learning. Consequently, because the effects of adaptation still remain evident after startle, there is clearly another center other than the brainstem centers. This also highlights how each purposeful reaching movement also has some component that can be attributable to a more primitive program triggered by the brainstem. This supports the concept of the society of mind [15], in which the brain is actually not one unit but multiple units that work in concert to function. This may also be the reason why neuroplasticity is successful after brain damage, because through practice, patients are able to reroute their commands through the remaining centers and pathways to achieve new functional ability.

Robustness to such effects (extinction) may be a way to gauge the extent of learning. Not all subjects were vulnerable to startle, so one may speculate that those were either not easily startled or they were perhaps further along in their learning process and had a more consolidated and robust performance as a consequence. It remains to be seen whether startle is more prevalent during the fragile early stages of learning where consolidation has not yet taken place.

The approach might also heighten motivation and/or attention not just in recall but also in the learning process itself, making more errors more noticeable. This study provides evidence that can point to future studies that attempt to exploit the natural adaptive tendencies in the nervous system for teaching new motor functions. These results can impact training areas such as piloting, teleoperation, sports, and rehabilitation.

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