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Degraded expression of learned feedforward control in movements released by startle

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Abstract

Recent work has shown that preplanned motor programs can be rapidly released via fast conducting pathways using a startling acoustic stimulus (SAS). Our question is whether the startle-elicited response might also release a recently learned internal model, which draws on experience to predict and compensate for expected perturbations in a feedforward manner. Our initial investigation using adaptation to robotically produced forces showed some evidence of this, but the results were potentially confounded by co-contraction caused by startle. In this study, we eliminate this confound by asking subjects to make reaching movements in the presence of a visual distortion. Results show that a startle stimulus (1) decreased performance of the recently learned task, and (2) reduced after-effect magnitude. Since the recall of learned control was reduced, but not eliminated during startle trials, we suggest that multiple neural centers (cortical and subcortical) are involved in such learning and adaptation. These findings have implications for motor training in areas such as piloting, teleoperation, sports, and rehabilitation.

Keywords

adaptation; learning; movement; upper extremity; healthy

I. Introduction

Learning to control movements in the face of differing environments and external disturbances relies on multiple modes of control. One component of interest is the feedforward motor plan, in which an internal model is used to predict the outcome of motor commands based on recent experience. Feedforward commands are used in a wide range of

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Conflict of Interest

The authors declare that they have no conflict of interest.

everyday actions, however very little is known about how these commands are represented in the nervous system, and whether or not they involve multiple parts of the brain.

Evidence supporting the existence of internal models that are preplanned comes from experiments challenging subjects to execute repeated movements within novel environments, such as those created using robotically produced force-fields (Gandolfo et al. 1996, Shadmehr and Mussa-Ivaldi 1994) or by using visual distortions (Wei et al. 1995, Flanagan and Rao 1995, Patton et al. 2006, Held and Schlank 1959, Krakauer et al. 2000). When exposed to these perturbations, subjects make movement errors that gradually attenuate as they practice and learn. When the perturbation is unexpectedly removed, errors are made that are nearly symmetrically opposite to those originally made. These “after-effects” provide evidence for the existence of the learned internal model that predicts the dynamics of the movement before it even begins. Due to the ability of internal models to adapt to unexpected changes in the environment, researchers have gained insights on such learning processes in feedforward control. While evidence suggests that the cerebellum plays a primary role in the formation and storage of internal models (Krakauer et al. 2004, Tseng et al. 2007), the neural mechanisms related to the recall of a newly formed internal model are unclear.

Experiments using a startling acoustic stimulus (SAS) have offered new insights into the preparation, initiation, and adaptation of ballistic responses in humans (Carlsen et al. 2004a, 2012; Maslovat et al. 2009; Valls-Solé et al. 1995, 1999). The presentation of SAS prior to, or coincident with an imperative “go” cue (GO) results in the involuntary, rapid release of a planned movement with onset times typically 80ms earlier than voluntary movements (Carlsen et al. 2004a, 2004b; Valls-Solé et al. 1995, 1999; for a review see Carlsen et al. 2011). This response is typically faster than any natural reaction time, even when subjects can anticipate the GO cue through repeated practice with a fixed delay before GO. Interestingly, the spatial and temporal characteristics of the movement sequence remain intact. The phenomenon of early movement release has been termed a “StartReact” response. The StartReact only occurs if the task is known beforehand, and thus can be preplanned (Carlsen et al. 2004b). Based on the early latency of the onset of movement, it has been proposed that SAS releases a pre-planned “*motor program*” via fast conducting brainstem pathways that bypass normal voluntary execution circuits; although the exact mechanism underlying the StartReact effect is a matter of debate (Valls-Solé et al. 1999, Carlsen et al. 2004a, Nonnekes et al. 2014, Marinovic et al. 2014, Maslovat et al. 2015). When a SAS is applied during movement preparation period (prior to the “go” signal), the stimulus can release both the intended voluntary movement, but also the anticipatory postural adjustments that accompany that movement (MacKinnon et al. 2007; Carlsen and MacKinnon, 2010; MacKinnon et al., 2013). This result suggests that at least for some movement types, movement preparation involves a progressive buildup of a feedforward motor plan (i.e. using internal models to prepare for the upcoming action) over time prior to its release.

Because such internal models are typically *learned*, startle may also reveal if these fast conducting pathways are associated with recently learned feedforward controls. Our preliminary adaptation experiments suggest that startle-evoked actions failed to preserve the

full learned responses, evidenced by reduced after-effects (Wright et al. 2009, 2011). However these results did not evaluate how performance was affected by startle, and were potentially confounded by startle-induced muscle co-contraction that may have also diminished the learned responses. Accordingly, here we show the results of an additional experiment designed to fully evaluate performance in a task where co-contraction cannot confound any effect. One possibility is that startle releases the fully intact movement that is learned through visuomotor adaptation. This would suggest that the feedforward motor program residing within these brainstem pathways also contains an internal model. Alternatively, startle could abolish recently learned responses, since cortical areas are vital to the recall of internal models. This study establishes the relationship between startle and the recall of short-term learning of skills, which may impact training areas such as military, sports, teleoperation and piloting.

II. Materials and Methods

A. Apparatus

Subjects made reaching movements to targets using a robotic planar haptics/graphics system (Fig. 1), presented previously (i.e., “manipulandum,” Patton and Mussa-Ivaldi 2002, Burgess et al. 2007). The robot allows planar movements in two dimensions and is able to record limb position at 200 Hz. An overlaying projector displayed the current position of the hand on a screen located in front of the subject in the coronal plane.

B. Startling Acoustic Stimulus (SAS)

An analog tone (1400 Hz, 40ms) was generated to create the SAS. The signal was amplified and presented via a loudspeaker (MG M-58H Horn Speaker) placed directly behind the subject with an intensity of 124dB (measured using a Brüel & Kjaer Precision Level Sound Meter Type 732A) (see Carlsen et al. 2011 for a review of startle methods).

C. EMG Recordings

Surface EMG was collected from the right anterior deltoid, posterior deltoid, long head triceps brachii, long head biceps brachii, and left sternocleidomastoid (SCM) using bipolar surface electrodes (Delsys Bagnoli). Data was digitally sampled at 1 kHz (National Instruments USP-6229) and continuously collected using a customized program written with 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 two-way Butterworth filter.

D. Protocol

Nine healthy adult subjects, free from neurological or musculoskeletal disorders and naïve to the learning paradigms participated in this study after signing a Northwestern University Institutional Review Board approved consent form. Subjects grasped the handle of the robot with the right hand and performed a series of horizontal planar reaching movements away from the body to a circular visual target (radius 18mm) located 15cm in front of a fixed start position. Chair height was adjusted so that the start position of the hand was located along the body midline, 20 cm anterior to the chin and 30 cm below the chin (approximately standard table height).

Each trial began with the cursor at the start position and the appearance of the intended target. After a 2.5s fixed time period, a low-level acoustic stimulus (83dB) was presented via a piezoelectric buzzer to indicate the imperative GO cue. Subjects were instructed to initiate movement as quickly as possible after the GO cue, and to execute the targeted movement in a smooth, straight manner as accurately as possible. Moving the limb resulted in the movement of a cursor on the screen. When the cursor stopped within the target (>0.5 s), the target changed color, denoting the end of the movement. The change in target color provided feedback on movement parameters. Specifically, the target turned green if the movement time (time from movement onset to the time the target was reached) was within the predetermined range of 450–700ms, consistent with typical movement times seen for 15cm movements (Kawato 1999). In addition, the word “Speed”, which was displayed in the top left-hand corner of the workspace, turned green if the peak velocity of the movement was within the range of 0.7–1.1 m/s. 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. Reaction time (the time between the presentation of the GO cue and when the handle velocity reached a threshold of 0.1m/s) was also displayed on the screen (in ms) after each trial to encourage fast reactions.

Each subject participated in a typical adaptation/learning paradigm that consisted of the following phases:

Familiarization—To become familiar with the experimental conditions, subjects performed 25 unperturbed straight-line movements to the target in response to GO. Based on previous testing this number of familiarization trials is sufficient for subjects to gain a basic level of understanding and proficiency in the task.

Baseline Testing—Subjects performed 5 unperturbed straight-line movements to the target in order to establish a baseline performance level before adaptation training began.

Initial Exposure—Subjects performed 40 targeted movement trials in which 5 trials contained a visual distortion (Cunningham 1989, Roby-Brami and Burnrod 1995, Krakauer et al. 2000), where any movement away from the start position resulted in the deviation of the cursor at a 45 degree angle in the clockwise direction with respect to the start position. This phase was conducted to assess the magnitude of the movement error induced by an unadapted visual distortion. Because the rotation distortion was centered at the starting position, subjects were unaware of the presence of the visual distortion until after the movement was underway.

Also during this phase, four of the nine subjects were exposed to SAS presented simultaneous with GO (5 trials). The number of SAS trials was kept low in order to avoid habituation (see Carlsen et al. 2011).

Training—Subjects performed 100 targeted movement trials with the consistent presence of the visual distortion. Subjects were instructed to attempt to move so that the cursor moved in a straight-line from the start position to the target. In order to achieve this, the subjects had to move to a location that deviated 45 degrees in the counterclockwise direction from

the target with respect to the start position. The last 5 trials were used to evaluate subjects' learned behavior in the presence of visual distortion (Control-performance trials).

Evaluation—To evaluate adaptation and after-effects that occurred following training, 200 trials were performed where the majority included the presence of visual distortion. In 15 of these trials subjects randomly experienced either the unexpected removal of visual distortion (Control-catch trials; 5 trials), or the unexpected removal of visual distortion accompanied by a SAS at 250 ms prior to GO (SAS-catch @ -250ms; 5 trials) or simultaneous with GO (SAS-catch @ -0 ms; 5 trials). Subjects were unaware of the removal of visual distortion until movement was underway. To evaluate the effects of SAS on learned behavior, visual distortion was randomly accompanied by SAS (SAS-performance trials) in 10 trials (5 trials with SAS at -250 and -0 ms each).

E. Data Analysis

In this movement task the anterior deltoid muscle acted as the initial agonist muscle, and hence premotor reaction time (RT) was defined as the time point when deltoid EMG activity exceeded two standard deviations above the average resting activity for at least 25ms. We visually inspected each trial to confirm the EMG onset and manually adjusted the time point when necessary. Premotor RT was measured relative to the onset of the GO cue for control trials and relative to the onset of the SAS for startle trials since SAS presented prior to the GO cue can cause a premature release of movement.

The detection of a StartReact response was strictly evidenced by two indicators. First, a burst of EMG activity in the SCM with an onset (determined using the algorithm described above) in the time window of 30–120ms relative to stimulus onset was considered to indicate a startle response (Carlsen et al 2011). Second, a short latency in the onset of movement (also termed *early release*) indicated a StartReact response whereby premotor RT in individual startle trials was considered to be *early* if it fell under the 95% confidence interval of the mean Premotor RT for Control-voluntary movements (last 25 trials in the “Training” phase). This criterion was implemented to exclude SAS trials where subjects might have been able to change their intended feedforward program following stimulus onset. All trials that exhibited both indicators -- startle-related SCM activity *and* an early release of movement -- were separated for analysis. Trials (8 in total) in which subjects launched their movement before the GO cue or SAS or stopped their movement prior to reaching the target were removed from analysis. Subject data sets without a StartReact response in at least one trial for each of the SAS conditions were removed from the analysis.

Angular deviation from a straight-line movement between the start position and the target was the primary measure of movement error. Initial Direction Error (IDE) was defined as the angle between the ideal straight line movement and the initial direction actually moved – calculated as the vector formed from the location at movement onset to the location reached 150ms into the trajectory.

E. Statistical Analysis

To determine if there was an effect of the SAS on motor release, we compared premotor RT between control and SAS trials. The two SAS timing conditions (SAS @ -250ms and SAS @ -0ms) in each of the SAS-performance and SAS-catch trials were combined for analysis since changes in premotor RT do not depend on the timing of the startle stimulus with respect to GO at these time points (Carlsen and MacKinnon 2010). One-way Analysis of Variance (ANOVA) was used to determine statistical differences between premotor RT observed in Control-voluntary movements (i.e. trials during the last 25 trials of the “Training” phase) and premotor RT observed in SAS-performance and SAS-catch trials during the “Evaluation” phase of testing.

Initial direction movement errors were analyzed using a 2 (visual distortion: performance, catch) x 3 (Stimulus: Control, SAS-0ms, SAS-250ms) repeated measures Analysis of Variance (ANOVA). Control trials from the end of the Training phase were used to provide data for the Control Performance trials (i.e. those *with* the visual distortion present), since these were not affected by the concurrent presence of catch trials in the Evaluation phase. All other data was derived from the Evaluation phase of testing. Movement errors for Performance trials were adjusted by applying a 45 degree rotation (i.e. measured from hand position) in order to statistically compare to those of Catch trials. Student’s paired t-tests were used to determine the locus of any differences. For all statistical calculations, we considered differences significant with α of 0.05.

III. Results

A. Evidence of StartReact responses

We first examined the influence of the startle stimulus on each subject (Table 1). Six of the 9 subjects exhibited a startle response, complete with an early release of movement and SCM activity, in a least one trial for each of the SAS conditions (85 out of 120 trials). The data from these six subjects were separated for analysis ($n = 6$).

Premotor RTs for the SAS-catch trials and SAS-performance trials were compared to Control-voluntary movements (i.e. the last 25 movements of training phase) (Fig. 2). One-way ANOVA revealed Premotor RTs differed across groups; $F(2,15) = 8.35$, $p = .0037$. Mean ($\pm$ SE) premotor RT in Control-voluntary trials was 143 ms (± 13 ms), and mean ($\pm$ SE) premotor RT for SAS-catch and SAS-performance trials were 90 ms (± 9 ms) and 88 ms (± 10 ms), respectively. Post-hoc analysis revealed that movements were initiated significantly earlier in both SAS-catch (mean change in RT = 53 ms) and SAS-performance (mean change in RT = 55 ms) trials compared to Control-voluntary trials.

B. Movement Errors reveal startle-induced alterations of learning

Trajectories observed in the different experimental phases were consistent with a typical adaptation paradigm (Fig. 3) (Shadmehr and Mussa-Ivaldi 1994). Across conditions, StartReact trials were associated with a reduction in after-effect magnitude when the visual distortion was unexpectedly removed (Fig. 3d, Fig. 4; Control-catch trials vs. SAS-catch trials) and a decrease in performance following training within the visual distortion (Fig. 3c,

Fig. 4; Control-performance vs. SAS-performance). A main effect of Stimulus was observed, $F(2,10) = 8.11$, $p = .008$, whereas no main effect of Visual distortion was observed, $F(1,5) = 0.23$, $p = 0.653$, and there was no significant interaction between the factors, $F(2,10) = 1.30$, $p = 0.314$. Post-hoc comparisons of stimulus condition (collapsed across visual distortions) showed that movement errors in the SAS-0 and SAS-250 conditions were significantly smaller than in the Control condition, $p < .05$, whereas the SAS conditions were not different from one another ($p = 0.56$).

One concern was that these effects may have been potentially biased by the movement direction, possibly because of biomechanical reasons or reflexes that differ in flexion and extension directions. To investigate this, we test three additional subjects in a reduced protocol using an opposite (counterclockwise) visual rotation. Here startle was administered only during catch trials. We found after-effects in trials in which a startle response was detected to be reduced in the opposite direction to those observed following adaptation to a clockwise rotation, but still towards baseline (Fig. 5).

IV. Discussion

Here we present results of a study that examined the effect of startle on the release of a recently learned internal model formed through operating in the presence of a challenging rotation of visual feedback. We found that in trials where an early release of the movement, or “StartReact” response, was observed, (1) the magnitude of the after-effects was reduced, and (2) performance of the learned task was reduced (Fig. 4). Such degradation in learned performance suggests that SAS releases some feedforward components of the response, but the startle-elicited response does not totally incorporate the internal model that arises in adaptive training. To the best of our knowledge, these results are the first to probe the effects of startle on learned reaching movements following sensorimotor adaptation.

Previous studies involving StartReact have consistently shown that the movement released early by a SAS is not significantly different in terms of internal EMG timing characteristics from the movement observed during control (non-SAS) trials (Carlsen et al. 2004b; Valls-Solé et al. 1999). In the current study a consistent RT shortening effect was observed following the SAS (Fig. 2), however, the present results contrast with previous studies that have used a SAS to examine the state of movement preparation and release because the SAS released a *distorted* or insufficiently rotated version of the adapted movement compared to control. One explanation for the current results is that the original action plan is modified by a corrective internal model (i.e. a “correction factor”) implemented following exposure to the visual distortion. While the correction factor is typically able to adapt much of the original planned trajectory in a small number of trials (Roby-Brami and Burnrod 1995, Krakauer et al. 2000), it is nevertheless not able to *fully* correct for the distortion even after 100–200 trials (see Fig. 3). This might suggest that the correction factor is still relatively weak (in terms of strength of neural connections) in comparison to the uncorrected model. For example, several studies have revealed that “fragile” internal models are susceptible to interference, and have identified factors that may disrupt learning or short term and long term retention of internal models (Gandolfo et al. 1996, Brashers-Krug et al. 1996). It has also been consistently shown that StartReact responses are often more “vigorous” in nature

(likely due to increased startle response-related activation), resulting in increased peak displacement, and quicker movements (Carlsen et al. 2013; Carlsen et al. 2004a). As such, if the uncorrected feedforward trajectory was weakly adapted by an applied learned internal model, startle may have simply activated the involved motor circuits to such a degree that, in comparison to control trials, the balance of activation was much more strongly weighted towards the original programmed trajectory than to the correction factor (since the neural pathways/connections are more highly developed). This would have led to the observed decrease in trajectory correction in SAS-Performance as well as decreased after-effects in SAS-Catch trials (Fig. 4). Alternatively, it may be that the SAS released some moderately corrected components of the planned response, perhaps those associated with initial trajectory and posture, but other components required for closed-loop control later in the trajectory were not released by startle. In order to determine if SAS itself resulted in systematic trajectory bias we performed a follow-up test in which subjects experienced the *opposite* visual rotation (i.e. counterclockwise). The after-effects in SAS-catch trials were also reduced (i.e. in the opposite direction towards baseline), consistent with the phenomenon of degraded after-effects from startle. We would also expect any movement bias to appear when SAS is administered during unperturbed reaching prior to training; however, we compared these reaches released by startle to baseline trajectories and found that there were no differences ($t_{0.05}(4) = .920$ $p = .410$).

Several previous studies have shown that simple changes in motor preparation due to learning could be accessed through the use of a StartReact response (Maslovat et al. 2009; Maslovat et al. 2008). The results of the current study suggest that trajectory correspondence between the startle-released response and Control trials in both performance and after-effects may be a way to gauge the *strength* of a learned internal model. However, for corrective internal models, several previous studies have suggested that feedforward control (as evidenced by after-effects), may be mediated by higher-level cognitive planning (Donchin et al. 2012, Imamizu et al. 2000, Maschke et al. 2004, Shadmehr and Smith 2005), particularly early in learning. Since startle reduced, but did not eliminate, the learned correction it may be that the strength of the higher level cognitive planning was not as accessible by the startle as the more automated uncorrected reach. We suggest that multiple neural centers (perhaps cortical and subcortical) are involved in such learning because the effects of adaptation still remain evident during startle trials. With increased learning, more of the higher level processing required to correct the initial trajectory may be incorporated into the circuits that are accessible by the startle.

In this experiment, it was evident that the level of vulnerability to startle varied among subjects. For example, some subjects exhibited many StartReact responses, complete with SCM activity and a significant decrease in premotor RT. However, the responses of many others met only one of the criteria used to define a StartReact response. Some previous studies have suggested that when a response is not (or *cannot* be) prepared in advance, the startle response in SCM habituates much more rapidly (Carlsen et al. 2003; Valls-Solé et al. 1997). Further to this, it has been suggested that the magnitude of the SCM response can be used as an index of preparatory activity in subcortical nervous system structures (Carlsen et al. 2008; Kumru et al. 2006). In *choice* reaction-time tasks, where subjects are required to

execute one of two different (but known) actions based on a cue, movement cannot be fully prepared in advance since subjects are unaware of the required response until the cue is presented (Carlsen et al. 2004a). In our particular case of reaching movements to targets, the task *was* known in advance of the GO, but the adapted response was nevertheless attenuated on SAS trials. This suggests that although the basic response was prepared, the corrective model may not have been strongly represented. As the extent and rate to which subjects learned the visual distortion varied, one may speculate that those who were either not easily startled or were perhaps less further along in their learning may have devoted more resources to the corrective portion that was not as accessible by the startle. It is noteworthy that when a secondary analysis was performed, which included all nine original subjects, and where the startle response criteria was more lenient (requiring only early release of movement; 129 out of 180 trials – see Table 1; mean ($\pm$ SE) premotor RT in Control-voluntary, SAS-performance and SAS-catch were 153 ms ($\pm$ 14 ms), 102 ms ($\pm$ 12 ms) and 98 ms ($\pm$ 12 ms), respectively; $F(2,24) = 6.18$, $p = 0.0068$), similar trends were found in trajectory deviations ($F(2,16) = 15.16$; $p = 0.0002$). This is consistent with previous startle investigations that have shown no differences in startle-evoked movement responses with and without SCM activity (Campbell et al. 2013; MacKinnon et al. 2007, Nonnekes et al. 2014, Reynolds and Day 2007, Tresch et al. 2014). However, including all the data may nevertheless introduce some spurious variability, as it is unclear without an overt startle response whether the produced trajectories are the result of the same mechanism (Maslovat et al. 2015) and/or a similar level of learning. It remains to be seen whether the incidence of observing a StartReact response is different during the fragile early stages of learning where consolidation of a learned task in memory has not yet taken place. More practice over an extended period of time (days or weeks) and/or a rest between practice sessions (known to better consolidate long term retention of skills; Brashers-Krug et al, 1996) would clarify if startle has an effect on a more consolidated motor memory.

One of the differences from this study and previous StartReact studies is that we failed to detect any relationship between after-effect magnitude and stimulus timing. Based on previous data (MacKinnon et al. 2007; MacKinnon et al. 2013), we expected a progressive build-up of a prepared response, such that a “more complete” response would be elicited by later stimulus times. It is possible that in the task used here, preparation does not progress in the same manner for reaching as it does for stepping. Furthermore, in this experiment, the time at which subjects began to prepare movements was uncertain. Recent research suggests that in situations where the timing information about when subjects were to release movements was relatively uncertain, movements were fully prepared well in advance to GO (Carlsen and MacKinnon 2010). Due to the length of the current experiment (as well as learning effects), the time at which subjects began to prepare the required action may have been delayed as subjects learned to respond faster to GO. Consequently, it is unclear whether the various SAS timing conditions released the feedforward program during different stages of build-up. Manipulating the response timing information such that the initial moment of movement preparation can be identified with more certainty may help clarify the time course and assembly of prepared movements following an adaptation task.

This study sheds light on how adapted actions are planned and executed when the movement skills have been acquired through repetitive practice. The evidence presented here suggests that higher level adaptive internal models are not fully incorporated into preplanned actions, and that the underlying (and unadapted) action retains particularly strong neural connections at least during the early part of learning. This information may be used to exploit the natural adaptive tendencies in the nervous system for teaching new motor functions, having an impact on a variety of training situations where acquired skills need to be recalled in spite of startling stimuli that reduce their effectiveness, such as piloting, defense, teleoperation, sports, construction, traffic, or rehabilitation.

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Fig. 1. Subjects performed targeted reaching movements using a two-planar robot called the manipulandum.

Fig. 2. Premotor reaction times (RT) relative to stimulus onset for SAS catch trials and SAS performance trials (the two SAS timing conditions were combined) compared to Control voluntary movements. Each dot represents a single trial. Subject individual trial data are separated into columns for each condition, means indicated by horizontal bars and 95% confidence intervals indicated by vertical bars. Group mean and 95% confidence intervals are indicated by a diamond shaped shaded area. Asterisks indicate significance.

Fig. 3.

A representative subjects' trajectories during the different phases of the experiment. (a) Baseline trajectories resembled straight lines. (b) Movement errors occur in the presence of clockwise visual distortion. (c) After training, subjects began to learn and revert back to straight line movements (black lines). SAS trials while within the visual distortion field showed an increase in movement error (-250ms and -0ms , gray) (d) After visual distortion was removed, trajectories became nearly mirror images of those seen in (b) (Control-catch, black). Trajectories were distorted in SAS catch trials (-250ms and -0ms , gray). All trajectories shown are that of the cursor position.

Fig. 4. Movement errors in SAS-catch trials (left) and SAS-performance trials (right) compared to Control-catch trials and Control-performance trials, respectively. SAS trials were associated with significantly reduced after-effects in catch trials and increased error during performance trials. Asterisks indicate significance. (Baseline trials are not shown for subject four)

Fig. 5. Trajectories for one subject that trained within a counterclockwise visual rotation. (a) Baseline trajectories. (b) Movement errors when initially exposed to the rotation. (c) Learned trajectories at the end of training. (d) After-effect trajectories during SAS-catch trials were distorted in the opposite direction than those using a clockwise rotation (see Fig. 3d), but closer to baseline than Control-catch trials (black). Only SAS-catch trials in which a startle response was detected are shown.

Table 1

Individual subject data indicating SAS trials in which a startle response was detected. Each box represents a startle trial. Trial condition is indicated by the top row (I – SAS @ –0ms, II – SAS @ –250ms, asterisk represents SAS with visual distortion). Only trials where SCM activity (indicated black dot) and an early release of movement (indicated by a shaded box) were observed were included in the data set. Bad trials are indicated by a “x”.

		Condition																					
		I	II*	I*	II	I*	II*	I*	I	I	II*	II	I	II	II*	I*	I*	II	I	II	II*		
Subject	1	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
	2			●	●	●	●	●	●	●		●		●	●	●			●		●		
	3	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●		
	4																				●		
	5	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
	6	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
	7	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
	8	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
	9	●		●			●			●						●					●		