

1 The nervous system uses nonspecific motor learning in response to
2 uncertain perturbations

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Abstract

We constantly make small errors during movement and use them to adapt our future movements. Movement experiments often probe this error-driven learning by perturbing movements and analyzing the after-effects. Past studies have applied perturbations of varying nature such as visual disturbances, position or velocity dependent forces and modified inertia properties of the limb. However, little is known about how the specific nature of a perturbation influences subsequent movements. For a single perturbation trial the nature of a perturbation may be highly uncertain to the nervous system, given that it receives only noisy information. One hypothesis is that the nervous system can utilize this rough estimate to partially correct for the perturbation on the next trial. Alternatively, the nervous system could ignore uncertain information about the nature of the perturbation and resort to a nonspecific adaptation. To investigate how the brain estimates and responds to incomplete sensory information, we test these two hypotheses using a trial-by-trial adaptation experiment. On each trial the nature of the perturbation was chosen from six distinct types, including a visuomotor rotation and different force fields. We observed that corrective forces aiming to oppose the perturbation in the following trial were independent of the nature of the perturbation. Our results suggest that the nervous system uses a nonspecific strategy when it has high uncertainty about the nature of perturbations during trial-by-trial learning.

33

34 **Introduction**

35 Most motor adaptation studies have used a blocked design where the same type of
36 perturbation is applied to human movements repetitively. Over a sequence of trials subjects
37 gradually learn to correct for visual perturbations (Redding et al., 2005; Dionne and Henriques,
38 2008), velocity-dependent force fields (Shadmehr and Mussa-Ivaldi, 1994), position-dependent
39 force fields (Tong et al., 2002), acceleration-dependent force fields (Hwang et al., 2006) as well
40 as more complicated force fields (Thoroughman and Taylor, 2005). The nature of these
41 perturbations (referring to what aspects of the movement are affected by the perturbation) varies
42 across studies. The general finding is that humans can eventually learn to generate a response
43 that roughly mirrors the perturbation and enables them to move as if they were not perturbed.

44 The learning in such experiments that repetitively use the same perturbation is usually
45 modeled as incremental learning. An implicit assumption of these models is that the nervous
46 system expects a related perturbation during the next movement. For blocked-design experiments
47 this assumption is valid; but we need to recognize that perturbations experienced during daily life
48 usually change frequently, and that even the nature of perturbation may vary over time. Imagine
49 you reach for a cup but fall short; this movement error can be a result of displacement of the cup,
50 or an incidental shove on your arm by someone. Perturbations of varying nature, either visual or
51 dynamic, can influence your movements randomly and you will make adaptation in subsequent
52 movements. How does the brain deal with such perturbations when they vary over time?

53 The trial-by-trial adaptation paradigm, which usually varies the perturbation amplitude
54 from trial to trial, is suitable to investigate this problem (e.g., Scheidt et al., 2001; Baddeley et
55 al., 2003; Fine and Thoroughman, 2007; Wei and Körding, 2009). The nature of perturbations

56 has not been systematically varied in this paradigm and little is known about how the nervous
57 system copes with diverse perturbations in such a setting. Here we examine the extent to which
58 the nervous system can estimate the nature of perturbations on a trial-by-trial basis for learning.

59 This work centers around two working hypotheses. Our first hypothesis derives from
60 state space models, which usually assume learning to be proportional to experienced
61 perturbations (Baddeley et al., 2003; Donchin et al., 2003; Fine and Thoroughman, 2007). These
62 models predict that adaptation is weak on a trial-by-trial basis and the after-effect mirrors the
63 preceding perturbation as a function of its nature. Our second hypothesis derives from recent
64 theoretical advances that emphasize that a perturbation is often ambiguous and its estimation is a
65 statistical inference problem (Berniker and Körding, 2008). This statistical account suggests that
66 in a trial-by-trial paradigm the nervous system may have uncertainty about the nature of
67 perturbations and would have to fall back on a nonspecific adaptation strategy.

68 Here we test how subjects adapt to perturbations of different nature, visuomotor rotations
69 or various force fields, in a trial-by-trial paradigm. Our results support the second hypothesis that
70 the nervous system employs a nonspecific adaptation strategy when it is uncertain about
71 perturbations of varying nature.

72

73 **Methods**

74 The present study includes two experiments that share identical protocol and
75 experimental setups, and similar data analysis. The primary difference between the two
76 experiments is how trial-by-trial learning is evaluated: in Experiment 1, catch trials without
77 perturbations were randomly interspersed with perturbation trials; in Experiment 2, catch trials
78 are implemented with an error-clamping force channel (Scheidt et al., 2000; Sing et al., 2009) to

79 probe the learning. We will first present methods of Experiment 1 in details and then introduce
80 Experiment 2 and its differences.

81 *Experimental procedure (Experiment 1)*

82 Eight naive subjects participated in Experiment 1 after providing informed consent. All
83 subjects were right-handed with normal or corrected-to-normal vision. All procedures were
84 approved by the institutional review board of Northwestern University.

85 The subjects were seated in front of a table and held the handle of a 2-D robotic linkage
86 with their right hand (Fig 1A, see elsewhere for detailed description, Shadmehr and Mussa-
87 Ivaldi, 1994). The hand could be moved freely, with low friction but was restricted to move in
88 the horizontal (transverse) plane of the robot. The seat height was adjusted for each subject to
89 keep the right arm at shoulder level. The right upper arm was also supported by a customized
90 harness hung from the ceiling to minimize the effect of fatigue and to keep posture constant. The
91 movement of the hand was measured by the manipulandum at 250 Hz, but vision of the actual
92 hand was obscured as the movement was performed underneath a projection screen which was
93 positioned horizontally at the neck level. Visual feedback of the hand position was given as a
94 projected cursor with a display frequency of 75 Hz. Each subject performed a total of 1008
95 reaching movements, resulting in approximately one hour of participation.

96

97 Insert Figure 1 here.

98

99 The starting position of the reaching movement was represented as a white cross at the
100 middle of the workspace, aligned with the midline of the seated subject. Each trial started when
101 the subject placed the cursor at the starting position. After the hand remained stationary at that

102 position for 1 second the trial started. A target, represented as a yellow circle of 0.6 cm diameter,
103 was displayed 10 cm ahead of the starting position while the cross representing the starting
104 position disappeared. Subjects were instructed to execute an accurate forward movement to the
105 target at that moment. Once the cursor had moved 10 cm in the y direction, the target changed
106 color, green if hit, red if not. Then the starting position was displayed again to signal the subject
107 to return the hand and start a new trial. On the way returning to the starting position, the cursor
108 display was turned off until the hand was within 2cm of the starting position. This omission of
109 visual feedback reduced visual calibration, which usually decreases the learning effect for the
110 visuomotor rotation condition. Subjects were paid 4 cents for each successful hit in addition to
111 the \$10 they received for participating in the experiment. Subjects were encouraged to make fast
112 movements and a text warning “too slow” would appear if they failed to finish the movement in
113 350 *ms*. They were also instructed that movements that were made too slowly would not be
114 rewarded, regardless of whether or not the target was reached. The small amplitude of the
115 reaching movement and the emphasis on short movement duration minimized any feedback
116 corrections within a reaching movement. Since the focus of the current study is on how subjects
117 adapt to a previously experienced perturbation, this serves to minimize any response to ongoing
118 perturbations.

119 Half of the movements were affected by one out of 6 possible perturbations that were
120 randomly selected while the rest of the trials were catch trials without perturbations (Fig 1B). In
121 the visuomotor rotation condition, the cursor location was displayed as if the visual scene was
122 rotated 15° around the starting position, either clockwise or counterclockwise. The remaining 5
123 types of perturbations were forces applied by the handle of the manipulandum orthogonal to the
124 line connecting the start and the target position. These forces were defined by the hand position

125 (Fig 1B): linear (ramp condition), piecewise linear (triangle condition) or sine waves of varying
126 frequencies (half sine, full sine and double sine conditions). The maximal force was 4N in the
127 ramp condition and 8N in the other four conditions. Each type of perturbations was presented 42
128 times, either in the left or right direction with equal chances, for a total of 504 perturbation trials.
129 504 catch trials (no perturbation) were interspersed with perturbation trials. The probability of a
130 perturbation trial following another perturbation trial was lower than chance and set to 30%
131 through a re-sampling procedure. In this way, the immediate adaptive effects for opposing the
132 perturbations can be assessed in catch trials while avoiding subjects' anticipation of catch trials.

133 *Experimental procedure (Experiment 2)*

134 Seven subjects were recruited in Experiment 2. Experiment 2 shared identical procedures
135 as in Experiment 1 with only one difference: catch trials were presented with strong error-
136 clamping force instead of zero force as in Experiment 1. This lateral force behaves like a channel
137 that clamps the lateral deviation of the hand movement by a restoring force defined as:

$$138 \quad F = K * x + D * v_x$$

139 Where x stands for lateral deviation of the forward movement and v_x for its velocity, K is a
140 spring constant that specifies the position-dependent restoring force (set at -6000 N/m) and D is
141 a damping constant that specifies the velocity-dependent restoring force (set at -250 Ns/m). The
142 parameter setting of this force channel is identical to the one used in a previous study (Sing et al.,
143 2009). The sampling frequency increased to 2000Hz to meet the high demands of producing
144 realistic force channel. The error-clamping force channel effectively limited lateral deviation
145 from a straight-line to about 1 mm. It has been proposed that the force invoked by the force
146 channel following a force perturbation is indicative of the learning-related predictive changes

147 (Sing et al., 2009). We thus analyze the force profile in catch trials to quantify the trial-by-trial
148 learning.

149
150 *Data analysis*

151 The position and velocity data in both directions were measured. In Experiment 1, the
152 earliest and latest parts of the reach ($y < 0.5$ cm and > 8 cm) were excluded from the analysis.
153 Due to the low friction and low inertia of the hand-held manipulandum, the hand randomly
154 drifted at the starting position (visually marked as a 0.6 cm disc in diameter) before the
155 movement is initiated. To minimize this effect, we excluded the first 0.5 cm movements. The
156 reason for excluding the last 2 cm of the movement is that our study focuses on the adaptation to
157 perturbations that exhibits itself as a predictive control, whereas the last segment of a reaching
158 movement is dominated by feedback control (see a similar treatment, Scheidt et al., 2001). The
159 other reason for this exclusion is that some subjects stopped movement somewhat short of the
160 target distance and our original code did not well control for that. In Experiment 2, we exclude
161 only 3mm of the initial movement trajectory as the force channel constrained the initial drift and
162 8mm of the trajectory end owing to improved movement-termination judgment in the data
163 acquisition program. Nevertheless, we argue that the exclusion of partial movement trajectory do
164 not affect our investigation of trial-by-trial learning. Trials where the subject did not complete
165 the full reaching movement in the y -direction were excluded (less than 5% of trials in both
166 experiments). Position and velocity data that were directly available from data acquisition were
167 filtered using a 4th order Butterworth low pass filter (cutoff frequency 12 Hz) before re-sampling
168 to obtain spatial trajectories characterized by 200 points that are evenly spread in the y direction.
169 The velocity data was differentiated to obtain the acceleration profile. In Experiment 2, the force
170 measured by force channels was not filtered.

171 Under normal circumstances without perturbation, the hand reaching does not produce a
172 perfectly straight path but show some asymmetry, which can be viewed as a bias existing
173 universally across all trials. Averaging all catch trials that did not follow perturbation trials
174 yielded a good approximation of the bias in the natural (asymmetrical) path of the subject's
175 reaching movement. This average was subtracted from each trial, effectively eliminating the
176 asymmetry. The perturbation trials and the catch trials following perturbations were grouped and
177 averaged according to conditions. To compare between these trajectories, linear correlation was
178 performed in a pair-wise fashion among conditions. Since we are only interested in how much
179 they are correlated and not in what direction they are correlated, only absolute values of the
180 correlation coefficients are reported.

181 To investigate the force developed in catch trials to cope with perturbations, we analyzed
182 acceleration trajectories which share the same form as force trajectories subjects produce at the
183 hand (Experiment 1) and force profiles invoked by the force channel (Experiment 2). We
184 performed most of our analyses on these data as they directly reflect the corresponding strategies
185 (forces) subjects developed to compensate for perturbations. Using the fact that these trajectories
186 are rather symmetrical for perturbations in the two opposite directions (Fig 2), we mirrored the
187 trajectory in the left of the workspace to the right and only analyzed the average trajectory of
188 these two trajectories. Mathematically this was achieved by subtracting the acceleration/force in
189 the left workspace from the acceleration/force in the right workspace. This averaging captures
190 the form of trajectory and also reduces the number of condition comparisons and we simply call
191 these averages the acceleration trajectory (Experiment 1) and the force trajectory (Experiment 2)
192 throughout the paper. Principal component analysis was performed on these trajectories from
193 different conditions to evaluate their similarities and differences.

194 To quantify how much the shape of the corrective response can be accounted by the just
195 experienced perturbation, we decomposed the acceleration/force trajectory in the catch trial into
196 two components, one is a scaled version of the acceleration/force trajectory in the preceding
197 perturbation trial and the other is a generic (common) trajectory across conditions:

$$198 \quad X_{catch,i} = \alpha X_{perturbation,i} + X_{generic}$$

199 $X_{catch,i}$ is the acceleration/force trajectory in the catch trial for the i th condition and $X_{perturbation,i}$
200 is the acceleration/force trajectory from the corresponding perturbation trial. These two
201 trajectories are available from the data. The other two variables can be fitted from the data:
202 $X_{generic}$ is the common acceleration/force trajectory that is shared by different perturbation
203 conditions; α is a weighting variable characterizing how much influence the perturbation trial
204 has on the compensatory response. We utilized expectation-maximization (EM) algorithm to fit
205 each subject's data separately. Visuomotor rotation was not included in this analysis since
206 acceleration trajectories in this condition are fairly small around zero in Experiment 1 (see Fig
207 3A) and EM algorithm does not converge on these small values, while there is no force
208 perturbation in Experiment 2. Thus, α is a 5 (conditions) \times 1 vector and $X_{generic}$ is a time-series
209 vector which has the same length as that of the acceleration/force trajectory. We are particularly
210 interested in the absolute amplitude of α : the larger it is, the more the corrective response is
211 related to the specific perturbation.

212 To understand what error information the nervous system uses to adapt, we calculated the
213 error measures proposed in recent studies on adaptation in reaching movements. These measures
214 include the absolute distance of the movement end position to the target (endpoint error), the
215 maximal lateral deviation of the hand away from the straight path connecting the starting
216 position and the target, the lateral deviation of the hand from the straight path at the time of

217 maximal speed, the integral of lateral deviations over the course of movement and, the
218 directional error from the straight line at the time of maximal speed (Krakauer et al., 1999;
219 Scheidt et al., 2001; Baddeley et al., 2003; Donchin et al., 2003; Lai et al., 2003; Osu et al.,
220 2003; Fine and Thoroughman, 2006; Cheng and Sabes, 2007; Fine and Thoroughman, 2007). We
221 subsequently regressed these measures in the perturbation trials to the first principal component
222 of acceleration/force trajectories in following catch trials. These linear regressions were
223 performed for each type of error measures separately and also for every possible combination of
224 two error measures, in search of the best correlation between error measures and adaptation. We
225 expect that relevant error measures will lead to significant correlations.

226 The force measured by using the error-clamp force channel has been proposed as a direct
227 readout of feedforward control signal (Sing et al., 2009). However, a range of studies have
228 suggested that goal-directed movement involves two separate control strategies: the early part of
229 the movement relies on feedforward control commands that are particularly relevant for trial-by-
230 trial learning investigated in the present paper; the later part of the movement relies on feedback-
231 based endpoint control to stabilize at the final goal (Dizio and Lackner, 1995; Sainburg and
232 Wang, 2002; Ghez et al., 2007; Scheidt and Ghez, 2007; Tseng et al., 2007). Based on these
233 early studies, we postulate that the force measured in catch trial carries the signature of
234 feedforward learning in the early segment of the movement which progressively declines
235 towards the movement end. To capture this change, we give weights to the force in catch trials
236 (Experiment 2) by multiplying with a ramp that linearly changes from 1 to 0 over the course of
237 the movement. Assuming one control scheme transitions into another, the force after this
238 treatment should resemble the acceleration trajectory measured in Experiment 1.
239

240 **Results**

241 In our experiment we measured the aftereffects of various perturbations (see Fig 2) on the
242 subsequent catch trials (no perturbation). The imposed perturbations lead to a sizable effect
243 during the movement on that trial (Fig 2, dashed). Subjects appear to adapt to the perturbations
244 and exhibit aftereffects in the opposite direction on the following trials when no perturbation is
245 applied as in Experiment 1 (Fig 2, solid). This kind of adaptation effect was expected and has
246 been described in many previous trial-by-trial (e.g., Scheidt et al., 2001; Fine and Thoroughman,
247 2006), and block-learning studies (cf. Kawato, 1999). In Experiment 2, the kinematic aftereffect
248 in catch trials is absent as the force channel constrained most of trials within a 1mm-wide
249 straight line (not shown).

250

251 Insert Figure 2 here.

252

253 For both experiments, the reach trajectories are fundamentally distinct in perturbation
254 trials. The visuomotor rotation leads to a linearly displaced cursor (Fig 2A, only data from
255 Experiment 1 is shown). Since the movements are relatively fast, and the presentation of
256 perturbations is random, the visually displaced cursor can only be taken into account during the
257 later part of the reach (not included in the analysis). The ramp perturbation leads to movements
258 that curve away from a straight line but its effect is very gradual (Fig 2B). The half sine
259 perturbation leads to trajectories that are perturbed in a roughly linear way (Fig 2C). The full sine
260 perturbation makes trajectories be roughly cosine shaped and towards the end of the movement
261 perturbs the hand back to the target (Fig 2D). The double sine perturbation roughly translates the
262 trajectory sideways (Fig 2E). Lastly, the triangle perturbation results in a quarter sine wave

263 trajectory (Fig 2F). All these perturbation effects are distinct and produce a range of trajectory
264 shapes, endpoint errors and errors at the time of maximal velocity. As such, the 6 perturbations
265 appear to produce a broad range of error information that the nervous system can incorporate in
266 the adaptation process.

267 As the perturbation effects are largely symmetrical, we collapsed the movement
268 trajectories averaging the aftereffect of the leftward perturbation with the negative aftereffect of
269 the rightward perturbation (see Method). As such we reduced the number of conditions and can
270 then quantitatively test the difference/similarity of visual errors between perturbation conditions
271 (Fig 3). Indeed the visual errors in perturbed trials look quite distinct (Fig 3A): pair-wise linear
272 correlation analyses yielded correlation coefficients between 0.27 and 0.98 with an average of
273 0.60 ± 0.06 (Fig 3B). This is in sharp contrast to the trajectory errors observed in the catch trials.
274 These movement trajectory appear rather straight (as if subjects aimed for different targets) and
275 stereotypical and the average correlation coefficient are high at 0.92 ± 0.01 (Fig 3C and 3D).
276 This coarse analysis thus suggest that visual errors resulted from different perturbations are quite
277 distinct but trial-by-trial adaptation is rather insensitive to these distinct perturbations.

278

279

Insert Figure 3 here.

280

281 To confirm that the *forces* experienced by subjects were distinct we analyzed acceleration
282 trajectories from perturbation trials (Fig 4, only data from Experiment 1 is shown). These
283 trajectories appear to be different in both amplitudes and shapes (Fig 4A-F). The visuomotor
284 rotation does not induce much lateral acceleration of the hand in the initial portion of these fast
285 reaching movements. The later, feedback-based corrections appear at the very end of these

286 movements and are not included in our analysis. The ramp force perturbation does not show
287 much effect either, since the disturbing forces are small during most of the analyzed movement.
288 All other force perturbations induce very characteristic acceleration profiles. We performed
289 linear correlation between the trajectories from different conditions in a pair-wise fashion (Fig
290 4G). Correlation coefficients (R) vary from 0.11 to 0.93; on average the correlations are
291 relatively small (0.58 ± 0.07), indicating the forces experienced on the hand are distinct across
292 perturbations. The smallest correlations were found between the ramp and half sine, the half sine
293 and double sine and the double sine and triangle (R values of 0.27, 0.11 and 0.28, respectively).

294

295 Insert Figure 4 here.

296

297 To address how the perturbations affect the corresponding corrective responses, we
298 examined the hand's acceleration/force profiles in catch trials. In Experiment 1, we find that
299 these acceleration trajectories look remarkably similar in shape across conditions (Fig 5A).
300 Recall that during catch trials the robot produced no forces, so the similar acceleration profiles
301 indicate subjects produced similar forces under all conditions. This is especially apparent when
302 the acceleration trajectories from all conditions are scaled by their own range and plotted
303 together (Fig 5B). This suggests that the nervous system may make nonspecific response to
304 distinct but randomly presented perturbations. It should be noted that “initial” accelerations
305 shown in the figure are not zero since these are accelerations measured at 0.5 cm into the
306 movement. Apparently, subjects adapted to the perturbations and decisively moved in the
307 opposite direction of the previous perturbation.

308 To test the similarity between catch trials from different conditions, we performed
309 correlation analysis on these acceleration trajectories in the same way as we did for the
310 perturbation trials. The correlation coefficient's average value across comparisons was $0.73 \pm$
311 0.03 . These correlation coefficients are significantly higher than those found across perturbation
312 trials (compare with data from Fig 4G; one-sided paired t-test, $p < 0.05$), indicating the corrective
313 responses are less different than the perturbation trials are. In Experiment 2, forces in catch trial,
314 measured by the force channel, are not as smooth as the acceleration trajectories (Fig 5C, black
315 traces). By assigning linearly decreasing weights to force trajectories (Fig 5C, red traces; see
316 Method) in accordance to findings from recent studies (Dizio and Lackner, 1995; Sainburg and
317 Wang, 2002; Ghez et al., 2007; Scheidt and Ghez, 2007; Tseng et al., 2007), the resultant forces
318 appear to closely resemble those acceleration trajectories in Experiment 1; and more importantly,
319 they also appear similar across different perturbation conditions. This similarity is apparent if
320 they are scaled to their ranges and plotted together (Fig 5D). Taken together, acceleration
321 trajectories and force trajectories measured in catch trials suggest that first-trial adaptations to
322 different perturbations are remarkably similar.

323

324 Insert Figure 5 here.

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329 If a catch trial mirrors its preceding perturbation, it should be more correlated with the

330 preceding perturbation than catch trials following other perturbations. We thus calculated pair-

331 wise correlations between perturbation trials and catch trials and displayed the correlation

332 coefficients in a matrix. This correlation was calculated on acceleration trajectory for Experiment

333 1 and on force trajectory for Experiment 2 (shown in Fig 6A and 6B, respectively). Note the

334 correlation between the perturbation trial and the catch can not be calculated for visuomotor
335 rotation condition in Experiment 2 as there is no force trajectory for this perturbation (Fig 6B). If
336 responses to perturbations are specific, the highest correlation coefficient for each row (one type
337 of perturbation trials vs. all 6 types of catch trials) should fall on the diagonal line of the
338 correlation matrix. However, this is in general not the case even when we count the second
339 largest correlation for each row. Instead, in Experiment 1 we find that catch trials following a
340 visuomotor rotation correlated highest with almost all perturbation trials (Fig 6A). Catch trials
341 following half sine force perturbation correlated the second highest with 4 out of 6 perturbations.
342 Similarly in Experiment 2, the highest or the second highest correlation usually falls off the
343 diagonal line of the correlation matrix (Fig 6B). We tested further whether these off-diagonal
344 correlations are significantly different from diagonal correlation values. The acceleration
345 trajectories from individual subjects were submitted to bootstrapping and correlation analysis
346 was subsequently performed. This bootstrapping could not be conducted for Experiment 2 as the
347 force trajectory for perturbation trials was the same across subjects. The average 95% confidence
348 interval of correlations in Experiment 1 (Fig 6A) was 0.051; while the average difference
349 between the largest correlation and the diagonal correlation was as large as 0.093 (excluding the
350 visuomotor rotation condition as it has the highest correlation value on the diagonal line).
351 Therefore this sanity check confirmed that the pair-wise correlation was indeed off-diagonal.
352 Taken together, these results further demonstrate that the compensations shown in the catch trials
353 are not specific to the perturbations.

354

355

Insert Figure 6 here.

356

357 Despite finding that corrective responses are remarkably similar across different
358 perturbations, they might still resemble (or mirror) the previous perturbations but to a very small
359 extent. If mirroring of preceding perturbations is evidenced, it will support that people indeed
360 learned the form of the perturbation in one trial. We thus decomposed the acceleration/force
361 trajectories in catch trials into two components: a generic trajectory for all conditions and a
362 weighted version of the specific acceleration/force trajectories in the preceding perturbation trials
363 (see Method). The weight (α) is an indicator of what percentage of the variance in the trajectory
364 shape can be explained by the just experienced perturbation (Fig 6C). This weight is not
365 significantly different from zero for all conditions except the ramp condition for acceleration
366 trajectory and the triangle condition for the force trajectory ($p < 0.01$ and $p < 0.001$, paired t-test),
367 further demonstrating the small or negligible contribution of specific force perturbations on the
368 corrective responses.

369 The weight (α) is small and close to zero; however, we might ask how negative the
370 weight could be in reality so that we would have had a significant chance (5%) of missing it.
371 This value sets the maximal strength of the specific adaptation that can be expected from our
372 data. The ramp condition, whose α has the largest deviation from zero, has less than 5%
373 probability of having an α that is more negative than -0.15 (bound obtained from Gaussian
374 statistics). Similarly for each of other conditions, α is no more negative than -0.04. Previous
375 studies have found that the size of first-trial error correction is of the order of 0.4 (Krakauer et
376 al., 1999; van Beers, 2009). Hence, the perturbation-specific component of the adaptation for
377 trial-by-trial perturbations thus seems to be smaller in comparison to the total error correction by
378 an order of magnitude.

379 To quantify the dimensionality of different perturbations and their corresponding
380 compensations we applied principal component analysis (PCA) to acceleration trajectories in
381 Experiment 1. Subsequently, we can investigate how different perturbation trials and their
382 subsequent catch trials are by comparing their principal components. This comparison was not
383 performed for Experiment 2 since perturbation forces were deterministic and we cannot calculate
384 PCA analysis on perturbation trials. The PCA was performed on acceleration trajectories for
385 each condition separately (data as shown in Fig 4 and Fig 5). For perturbation trials, the first and
386 second components explain $81.0 \pm 2.6\%$ and $14.7 \pm 2.1\%$ of the total variance across conditions,
387 respectively. For catch trials, the first two components explained $71.5 \pm 3.1\%$ and $23.8 \pm 3.4\%$
388 of the total variance, respectively. Hence most of variance in the acceleration profile can be
389 explained with two PCA components for our data set. Central to our study, we want to know
390 whether perturbations employed in our experiment generated distinct perturbing effects and
391 whether the corrective responses are indeed similar across these perturbations. To compare
392 conditions using the principal component analysis, a standard procedure is to calculate the angles
393 between these PCA components. If these conditions are very different, the components should
394 orient orthogonal to each other with an angle close to 90 degrees. On the other hand, if they are
395 similar, the angle between components should be close to zero (Krzanowski, 1979). The pair-
396 wise comparisons of 6 conditions yield 15 angles. If the first two largest PCA components are
397 considered, perturbation trials yield an average angle of $13.3 \pm 4.2^\circ$ and catch trials yield $4.2 \pm$
398 0.8° . One-way ANOVA indicated that the angles between perturbation trials are significantly
399 larger than those between catch trials ($p < 0.005$). In order to conclude that angles between catch
400 trials are small while the angles between perturbation trials are large, we performed permutation
401 test to see what angles can be expected from a random set of acceleration trajectories. All the

402 acceleration trajectories in the analysis above were randomly regrouped into 6 conditions and
403 then relative angles were calculated based on this permuted data set. We performed this
404 calculation 1000 times. The average angle from the permutation test is 5.8° for perturbation
405 trials and 6.2° degrees for catch trials. For perturbation trials, the angle from the real data set is
406 significantly larger than the permuted one ($p < 0.0001$; p value is calculated as percentage of
407 angles from permutation tests that are larger than the angle from real data set; this definition of p
408 value is more appropriate as it does not require an assumption of normality). For catch trials, the
409 angle from the real data set is near the 95% percentile of the angles from permutation test ($p >$
410 0.95). This indicates the angles between perturbation trials are indeed large while the angles
411 between catch trials are indeed small. Taken together, by comparing the acceleration trajectories
412 from different conditions using PCA, we found that perturbation trials are rather distinct while
413 the corresponding corrective responses are rather similar.

414 If the nature of a random perturbation has no impact on the form of the corrective
415 response, we may then ask which aspects of movement errors give rise to the observed
416 responses. The kinematic errors (Fig 3) and the forces (by experimental design) experienced by
417 subjects for different perturbations are dramatically different and may be correlated with
418 adaptation. To quantify this, we performed a linear regression between various kinds of error
419 measures (see Methods) and the first principal component of the acceleration/force trajectory in
420 catch trials. The reason to use the first PCA component is that the acceleration/force profiles
421 from different conditions appear to be scaled versions of the same trajectory and the first PCA
422 components, which presumably indicate the amplitude of scaling, captures most of the variance
423 ($71.5 \pm 3.1\%$ and $60.3 \pm 3.8\%$ for acceleration and force trajectories, respectively). We
424 computed the error measures popular in studies of hand reaching, including end point error,

425 maximal lateral deviation from a straight line, deviation from a straight path at the time of
426 maximal velocity, integral of deviations from a straight line, directional error at the time of
427 maximal velocity, maximal lateral force applied (zero for visuomotor rotation condition) and
428 maximal lateral acceleration. Surprisingly, none of these correlations yielded significant results
429 and this result was consistent across all subjects. We also correlated the first principal component
430 to all possible combinations of two different error measures. No systematic results could be
431 found. This lack of correlation can be illustrated by the scatter plots where the first principal
432 component is plotted as a function of some selected error measures (Fig 7). This, from yet
433 another angle, suggests that subjects' response to perturbations is not specific, and largely
434 independent of the type of perturbation experienced.

435

436 Insert Figure 7 here.

437

438 The brain may not generally use non-specific adaptation in the cases we studied but it
439 might gradually learn to use them over the course of the experiment (meta-learning). If this is the
440 case, the non-specific corrections would not be fundamental but rather the result of learning the
441 statistical distribution of perturbations. If meta-learning was the reason then the corrective
442 responses at the beginning of the experiment should be different from those at the end of the
443 experiment. We thus compared the pair-wise correlation between the first and the second trial,
444 the first and the middle trial and the first and the last trial. These 3 correlation coefficients serve
445 as measures of how similar later after-effects are with earlier ones. Meta-learning should lead to
446 decreasing correlation over time. For both experiments, two-way ANOVA (3 timing \times 6
447 conditions) did not identify evidence of learning with the main effect of timing ($p = 0.58$ and

448 0.32 for Experiment 1 and Experiment 2, respectively). Neither main effect of perturbation
449 conditions ($p = 0.61$ and 0.34 for two experiments, respectively) nor interaction effect ($p = 0.96$
450 and 0.29) were significant. Secondly, we performed the decomposition analysis to parse each
451 trajectory (the first, the middle and the last trial) into a generic component and a perturbation-
452 specific component (see above and also in the Methods). The specificity should increase over
453 these trials if meta-learning is in effect. However, again, two-way ANOVA over the weight of
454 specificity (α) did not find any significant effect on timing ($p = 0.24$ and 0.86 for Experiment 1
455 and Experiment 2, respectively), perturbation ($p = 0.07$ and 0.96) and their interaction ($p = 0.23$
456 and 0.99). Note that the analyses of meta-learning here also did not find any significant
457 difference between perturbation conditions, in accordance to various results reported above. It
458 does not appear that meta-learning strongly affected our results.

459

460 **Discussion**

461 We have used a random sequence of perturbations to analyze trial-by-trial adaptation. We
462 have found that corrections from trial to trial depend on the main direction of a perturbation but
463 are similar regardless of the nature of the previously experienced perturbation. This finding
464 suggests that the responses to random perturbations are nonspecific to the form of the
465 perturbation, at least for the diversified position-dependent force perturbations and visuomotor
466 rotation explored in the present study. We find that the shape and magnitude of these nonspecific
467 responses are not significantly correlated with a number of error measures in the previous trial.
468 Our results thus indicate that during trial-by-trial adaptation with random perturbations, although
469 the nervous system learns to oppose perturbations, it does so in a manner that is independent of
470 the specific nature of the perturbations.

471 Our findings differ from the predictions of typical state space models in trial-by-trial
472 adaptation (Baddeley et al., 2003; Donchin et al., 2003; Fine and Thoroughman, 2007). These
473 models usually assume that the nervous system linearly adapts to each movement error. When
474 the same perturbation is applied repetitively, these models generally predict an exponential
475 learning curve towards complete adaptation, which has been observed in various motor
476 adaptation studies. With block learning subjects can produce forces that very well cancel force
477 perturbations such as a velocity-dependent force field (Shadmehr and Mussa-Ivaldi, 1994;
478 Thoroughman et al., 2007), position-dependent force field (Tong et al., 2002) and altered inertial
479 property of the limb (Krakauer et al., 1999). They can also produce movements that cancel a
480 visual perturbation such as a visuomotor rotation (Pine et al., 1996; Ghahramani and Wolpert,
481 1997). For trial-by-trial adaptation to perturbations of varying nature, state space models
482 similarly predict a partial learning for each perturbation and a small adaptive response as a
483 function of the perturbation. However, our study did not find any miniature mirroring of the
484 preceding perturbation in adaptive responses. The spatiotemporal features of these responses
485 remain rather stereotypical for different perturbations. Multiple factors might contribute to this
486 nonspecific adaptation to random perturbations – which we will discuss in the following
487 paragraphs.

488 One relevant factor may be limitations of the perceptual system (proprioception in
489 particular) for sensing the perturbing force. This may prevent the brain from estimating the exact
490 form of a perturbation in a single trial. This can be the case for the five position-dependent force
491 fields employed in this study. However, for the visuomotor rotation, there is no need to rely on
492 proprioception as the perturbation is visual. Despite the typically high precision of visual
493 information, the correction following a single visuomotor rotation was still partial and, more

494 importantly, indistinguishable from corrections for other perturbations. This suggests that when
495 the perturbation is perceived precisely, the nervous system still seems uncertain about the
496 perturbation. On the other hand, it is relatively easy for the nervous system to detect the direction
497 of the perturbation as such the subsequent compensation always opposes the direction of the
498 previous perturbation.

499 Sing and colleagues proposed that the lack of specific adaptation is due to the similarity
500 between seemingly different force perturbations in the context of muscle spindle signals (Sing et
501 al., 2009). This view is similar to our conjectures that limitation of the perceptual system is the
502 reason underlying the nonspecific response. However, as contrary to our finding of similar
503 adaptation to different perturbations, they found that distinct force fields (position-, velocity-
504 dependent or combinations of both force fields) could induce different first-trial learning
505 patterns. One possible reason for this discrepancy is that they presented a type of perturbation
506 intermittently, only with wash-out trials (without force perturbations) and error-clamp trials in
507 between. Through meta-learning subjects in the Sing et al.'s study may have learned about the
508 way the experiment was evolving. As our study has an unpredictable distribution of perturbations
509 it turns out that in our case meta-learning should favor a behavior in which learning largely goes
510 away – which we did not observe. As a result, subjects in their experiment could compensate for
511 different perturbations without much uncertainty about the nature of the perturbation. In the
512 current study, we presented subjects with random perturbations, which rendered subjects with
513 large uncertainty about incoming perturbations which may have lead to the observed nonspecific
514 adaptation.

515 The lack of specificity in trial-by-trial adaptation might suggest that forming an accurate
516 internal model needs repetitive exposure to the same perturbation. In perturbation studies with

517 block design, subjects gradually change their compensation (in terms of movement trajectory or
518 force profile) to “mirror” the perturbation (e.g., Shadmehr and Mussa-Ivaldi, 1994), indicating
519 that forming an internal model involves an incremental learning process. It has been recently
520 proposed that an optimal strategy for motor adaptation demands estimation of perturbations, a
521 process that involves a statistical inference based on noisy percepts (Berniker and Körding,
522 2008). In this model a sequence of trials is needed for the nervous system simply to be able to
523 determine the nature of a perturbation. Our results suggest that the brain cannot adapt well if
524 multiple exposures to a single type of perturbation are interspersed by other perturbations.

525 Two other studies on motor perturbation provided indirect support for the statistical
526 inference account for estimating perturbations. Fine and Thoroughman perturbed subjects’
527 forward reaching movements either to the left or to the right by velocity-dependent force (Fine
528 and Thoroughman, 2007). For some conditions the directions of random force perturbations were
529 either equally likely or biased to one side. For the other condition, the direction of the
530 perturbation was fixed but the occurrence of the perturbation was varied from rarely to more
531 often. They found that adaptation to perturbations were more pronounced when the perturbation
532 were more biased to one direction or applied more frequently. From our statistical account, this
533 increasing directional bias and occurrence of the perturbation make the nervous system more
534 certain about the form of the perturbation. In turn, the nervous system is more ready to adapt to
535 the perturbations. Braun and his colleagues (2009) recently examined how subjects adapted to
536 visuomotor rotation perturbations where the angles of the rotation were unpredictable (Braun et
537 al., 2009). They found that over a few learning trials subjects’ correction converged to
538 stereotypical patterns. The results of these two studies, along with findings of the present study,

539 suggests that the perturbation itself is not the only determinant for adaptation and the statistical
540 property of the perturbation sequence also shapes the compensatory response.

541 Previous studies have suggested that motor learning involves multiple processes adapting
542 at different rates to disturbances of comparable time scales (Smith et al., 2006; Körding et al.,
543 2007; Berniker and Körding, 2008). The observable learning effect is thus a combination of
544 multiple processes. In the present study the perturbations vary frequently from trial to trial and
545 potentially lead to learning that is dominated by fast responses. We provide evidence that
546 adaption on this fast time scale is nonspecific to the spatiotemporal pattern of the perturbation
547 but rather consistent for countering the direction of the perturbation.

548 The finding of nonspecific adaptation also has implications for error reduction that are
549 commonly reported in motor adaptation studies. A general finding in blocked-designed studies is
550 that the second trial after initial exposure to a perturbation, the trial equivalent to the catch trial
551 of our trial-by-trial design, already exhibits substantial improvement in performance. For
552 example, the initial error after imposing visuomotor rotation perturbation is reduced by about
553 40% in a single trial (Krakauer et al., 1999). Similarly, in a reaching experiment without
554 perturbations 46% of endpoint error is corrected in the second trial (van Beers, 2009). In our
555 study, we did not evaluate the error reduction (endpoint errors for example) as it involves
556 feedback-based correction at the end of reach. Instead, we are interested in how much people
557 learn from random perturbations and how much they shape their correction accordingly in the
558 following trial. Interestingly, the trajectories of catch trials have minimal resemblance to the
559 spatiotemporal signature of perturbations. This result thus suggests that large error reduction in
560 initial learning does not necessarily require formation of a “partial” internal model of the just-

561 experienced perturbation. Feedback-based error correction can be a large contributor to the error
562 reduction in early learning.

563 Our results also suggest that the first reaction of the nervous system to perturbations is to
564 act to impede their influences, regardless of the exact nature of the perturbation. Indeed, such
565 behavior has been shown during adaptation of reaching movements in an unstable force-field
566 (Osu et al., 2003). Osu et al found that subjects would move their hands in the opposite direction
567 of the previous perturbing force, even though this strategy was inappropriate and would lead to
568 movement errors. It was only after extensive training that they were able to reduce errors by
569 increasing the impedance of the arm. The sensitivity to the direction but not the nature of the
570 perturbation is consistent to the finding that after-effects during trial-by-trial adaptation are
571 categorical (Fine and Thoroughman, 2006). All perturbations in that study were brief force
572 pulses pushing the hand to the left or right randomly at different locations on the movement
573 trajectory. The compensatory response in the next trial was also found to be in the opposite
574 direction of the perturbation without dependence on the location and the magnitude of
575 perturbation. However, here we have shown that such stereotypical trial-by-trial adaptation is not
576 only relevant for force pulses applied at different positions along a movement trajectory but also
577 for a wide range of different perturbations. Most interestingly, our study also show that
578 adaptation to visuomotor rotation, a perturbation having no external force applied and thus
579 leading to no perturbed spindle signals, is indistinguishable from adaptation to various force
580 fields.

581 Recent findings of complex spike activity of Purkinje cells in cerebellum might serve as
582 the neural basis of a categorical adaptation strategy. Cerebellum has long been associated with
583 motor adaptation and complex spike activity has been postulated to be error signals that drive the

584 adaptation (Marr, 1969). Soetedjo and Fuchs measured the activity of Purkinje cells in the
585 vermis of the oculomotor cerebellum when monkeys performed a saccadic adaptation task
586 (Soetedjo and Fuchs, 2006). In this adaptation task, the visual target jumped during saccades and
587 the monkey adapted to this perturbation gradually over trials (McLaughlin, 1967). Similar to the
588 perturbations used in our reaching experiment, their perturbations were also randomly presented
589 in two opposite directions. They found that complex spike activity of adaptation-related Purkinje
590 cells was highly modulated by the direction of the error. However, the complex spike activity did
591 not show consistent changes when the error was progressively reduced over adaptation to
592 repetitive perturbations. It appears that the error signal driving the adaptation is insensitive to the
593 error size but sensitive to the direction of the perturbation. This is consistent with our behavioral
594 findings that hand movements always oppose the previous perturbation directionally but do not
595 depend on the nature of the perturbation. If the same complex spike activity pattern can be
596 found during adaptation of voluntary reaching movements, it will not only provide
597 neurophysiological underpinnings for our findings but also speaks to a common role of complex
598 spikes in motor adaptation across various tasks and motor effectors.

599 This experiment aimed at examining how subjects exhibit specific adaptation to different
600 types of perturbations in a trial-by-trial paradigm. We instead found that, under these conditions,
601 subjects adapt to perturbations in a nonspecific way. This study raises a good number of
602 questions. For instance, how does the transition from non-specific trial-by-trial adaptation to
603 specific blocked adaptation occur? Are there different brain areas involved? And, how could
604 current models of motor adaptation, such as state space models, be modified to fully account for
605 these results? Answers to these questions will constitute new constraints on the mechanisms used
606 by the nervous system for motor adaptation.

607

608

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687

688

689

690

Figure Caption

691

692 Figure 1: *A). Sketch of the manipulandum and the experimental setup. B-G) Six different*
693 *perturbations are shown in both left and right directions. The target is 10 cm away in depth*
694 *direction (Y direction) and all the perturbations are applied in the lateral direction (left and*
695 *right, X direction). Note for the visuomotor rotation (shown in panel B) the X axis is for*
696 *displacement and it is different from other panels where X axis is for applied perturbation force.*

697

698 Figure 2: *Average of the hand trajectories from perturbation trials and subsequent catch trials*
699 *are shown for different perturbation conditions separately. The perturbation trials are shown as*
700 *dash lines and the catch trials as solid lines. Trials with left perturbations are shown in black*
701 *and right in grey. The grey color shades stand for the standard error across subjects. Note in the*
702 *first panel that shows the visual perturbation condition, the perturbation trajectories are the*
703 *displayed visual feedback, instead of the actual hand trajectories. Data are only from*
704 *Experiment 1; Experiment 2 produced similar data for perturbation trials but its catch trials*
705 *have constrained the lateral deviation within 1mm (not shown).*

706

707 Figure 3: *A) and C). The visual trajectories (in the lateral direction) in perturbation trials (A)*
708 *and in catch trials (C) are plotted for different perturbation conditions separately. The black*
709 *lines are the subject average and the grey shadowed areas (often tiny) indicate the standard*
710 *errors across subjects. B) and D). Correlation coefficients from cross-correlation analysis of*
711 *visual trajectories resulted from perturbed trials (B) and catch trials (D) are plotted as a matrix*
712 *of gray shades. The correlation varies widely across pair-wise comparisons for perturbed trials,*

713 *but on average they are low, indicating distinct perturbation effects. On the other hand, the*
714 *correlation coefficients for catch trials are much higher, indicating similar one-trial learning*
715 *across conditions. Data are from Experiment 1; Experiment 2 does not permit analyses of*
716 *trajectories as it constrained the lateral movements in catch trials by applying strong force*
717 *channels.*

718

719 *Figure 4: A-F). The acceleration trajectories (in the lateral direction) in perturbation trials are*
720 *plotted for different perturbation conditions separately. The black lines are the subject average*
721 *and the grey shades (not very visible) stand for the standard error across subjects. G).*

722 *Correlation coefficients from cross-correlation analysis of acceleration trajectories resulted*
723 *from different perturbations are plotted as a matrix of gray shades. The correlation varies widely*
724 *across these pair-wise comparisons, but on average they are low, indicating distinct*
725 *perturbation effects. Data are from Experiment 1; Experiment 2 used identical perturbations and*
726 *thus produced similar data.*

727

728 *Figure 5: A). The acceleration trajectories (in the lateral direction) in catch trials from*
729 *Experiment 1 are plotted for different perturbation conditions separately. The black lines are the*
730 *subject average and the grey shades stand for the standard error across subjects. B). The same*
731 *acceleration trajectories as shown in Panel A are scaled according to their own range and*
732 *stacked together. Each line is from a single condition. C). The force trajectories (in the lateral*
733 *direction) in catch trials from Experiment 2 are plotted for different perturbation conditions*
734 *separately. The black lines are the subject average and the grey shades stand for the standard*
735 *error across subjects. The red lines denote the forces that are calculated by multiplying the raw*

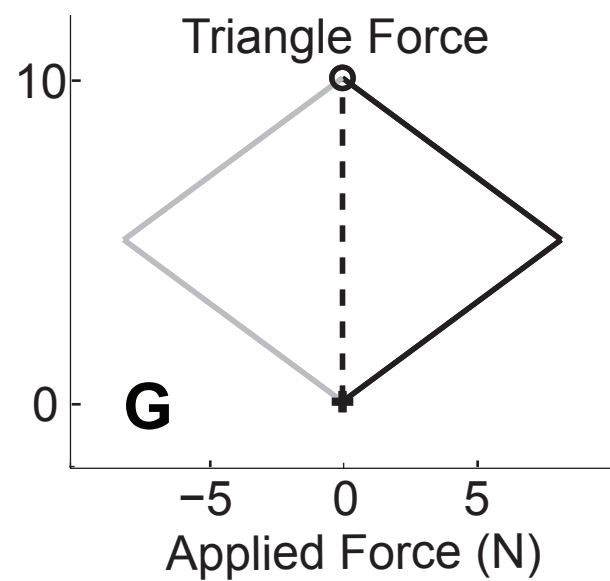
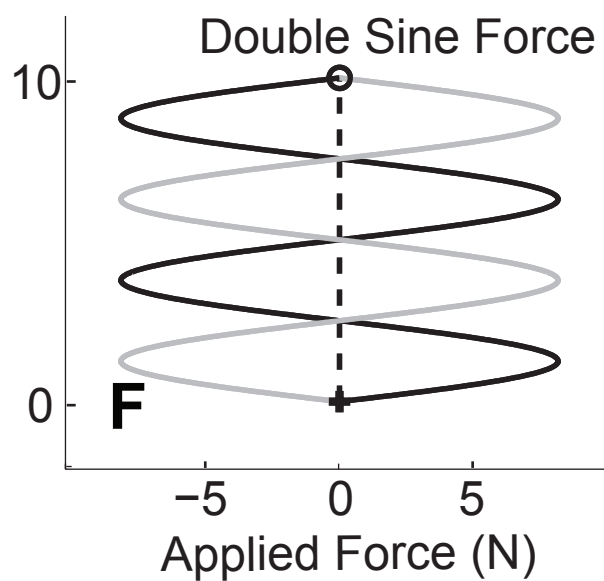
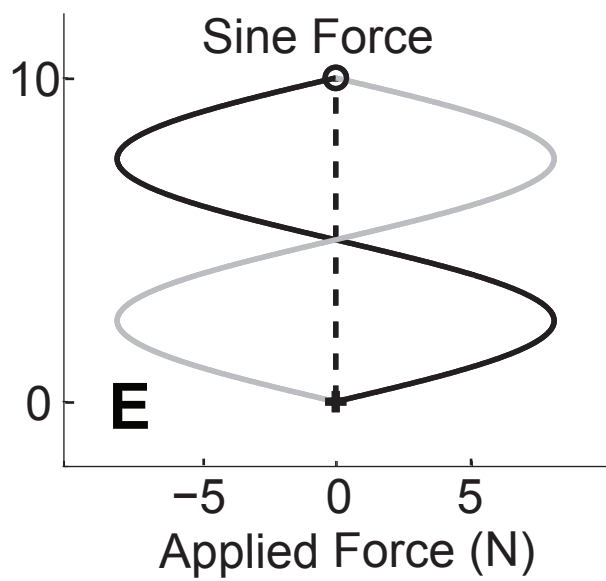
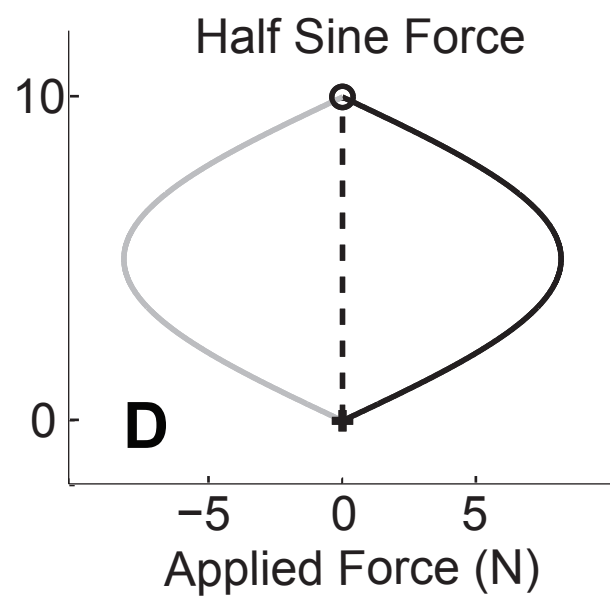
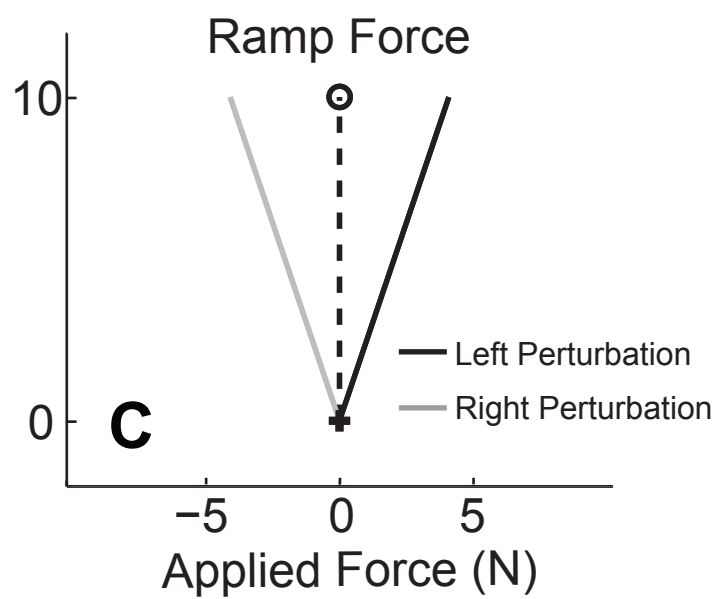
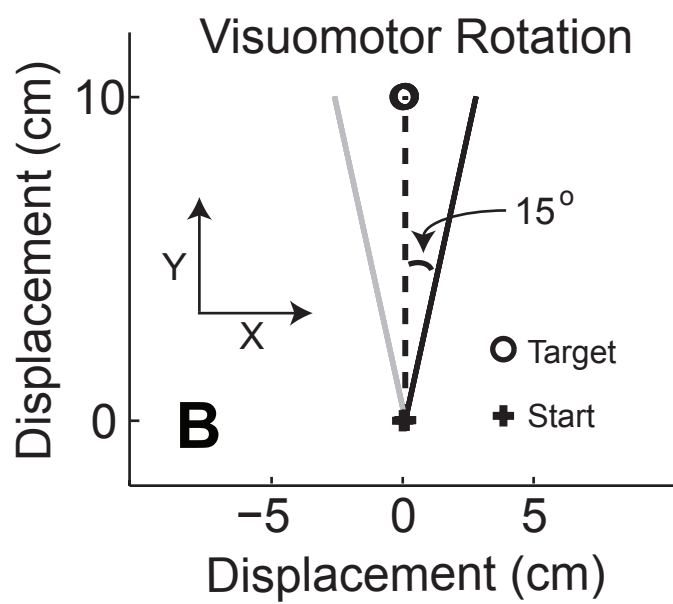
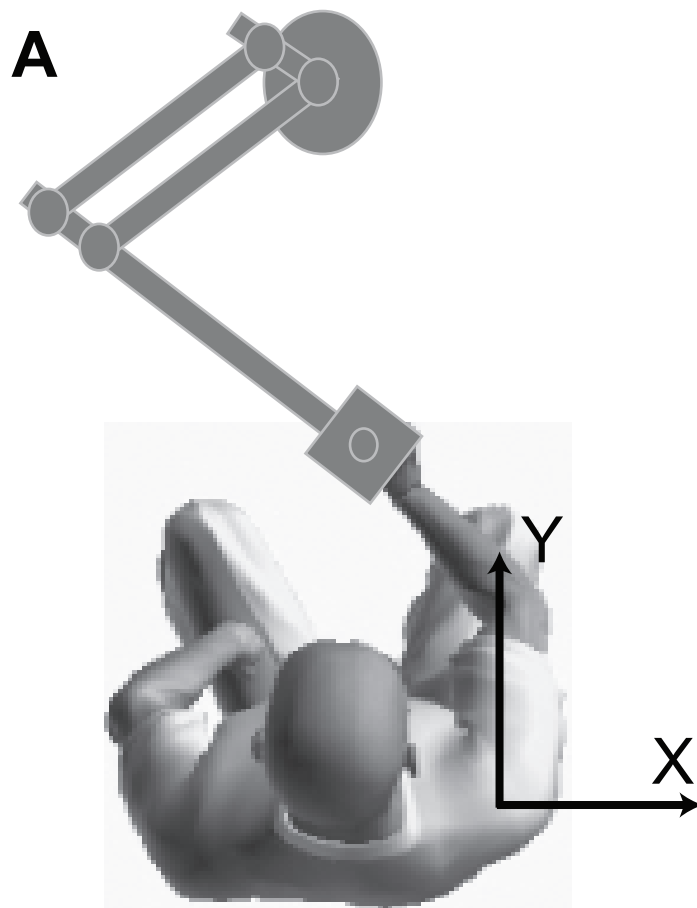
736 force with decreasing gains (see Method). D). The force trajectories as shown in panel C are
737 scaled according to their own range and stacked together. Each line is from a single condition.

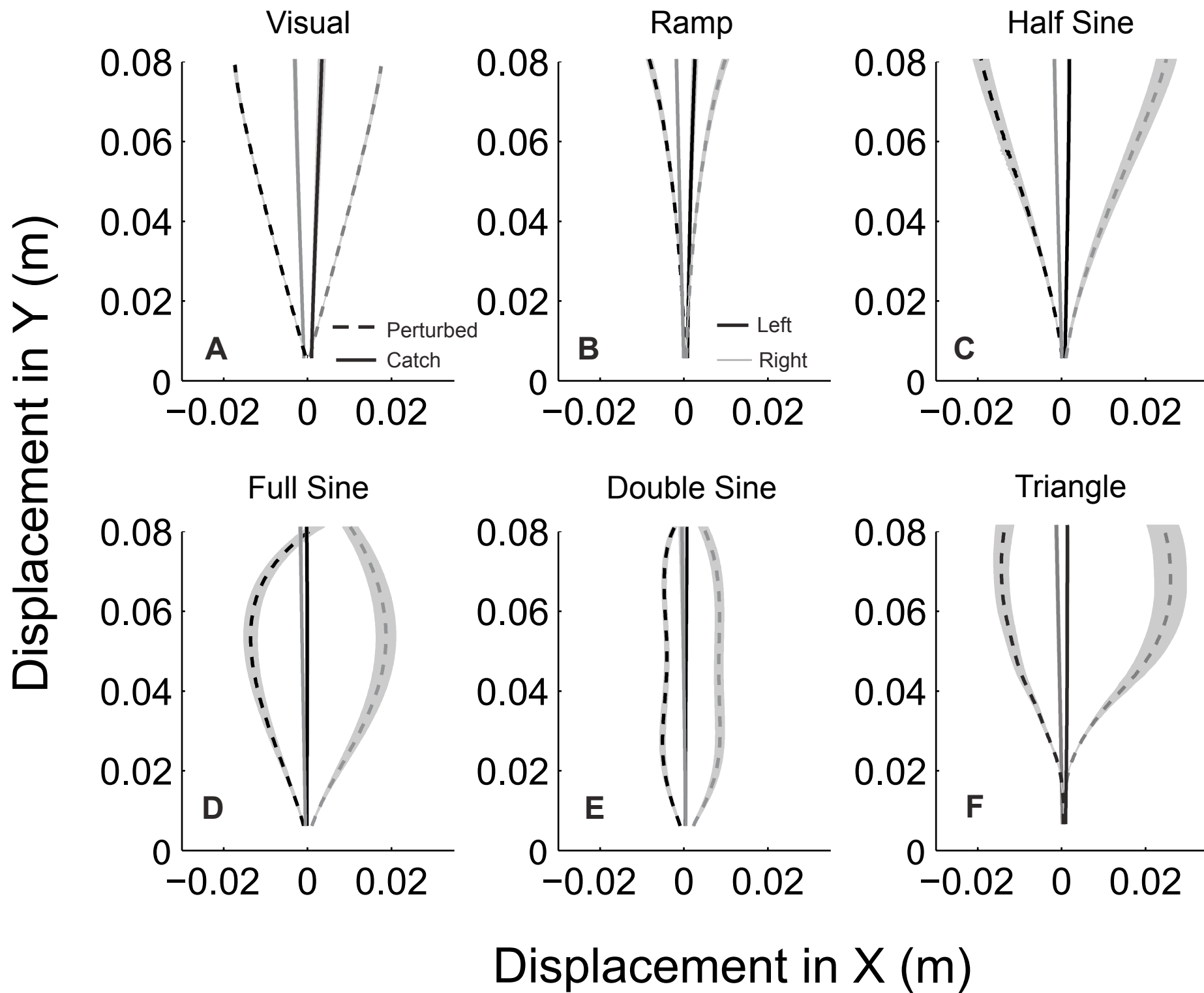
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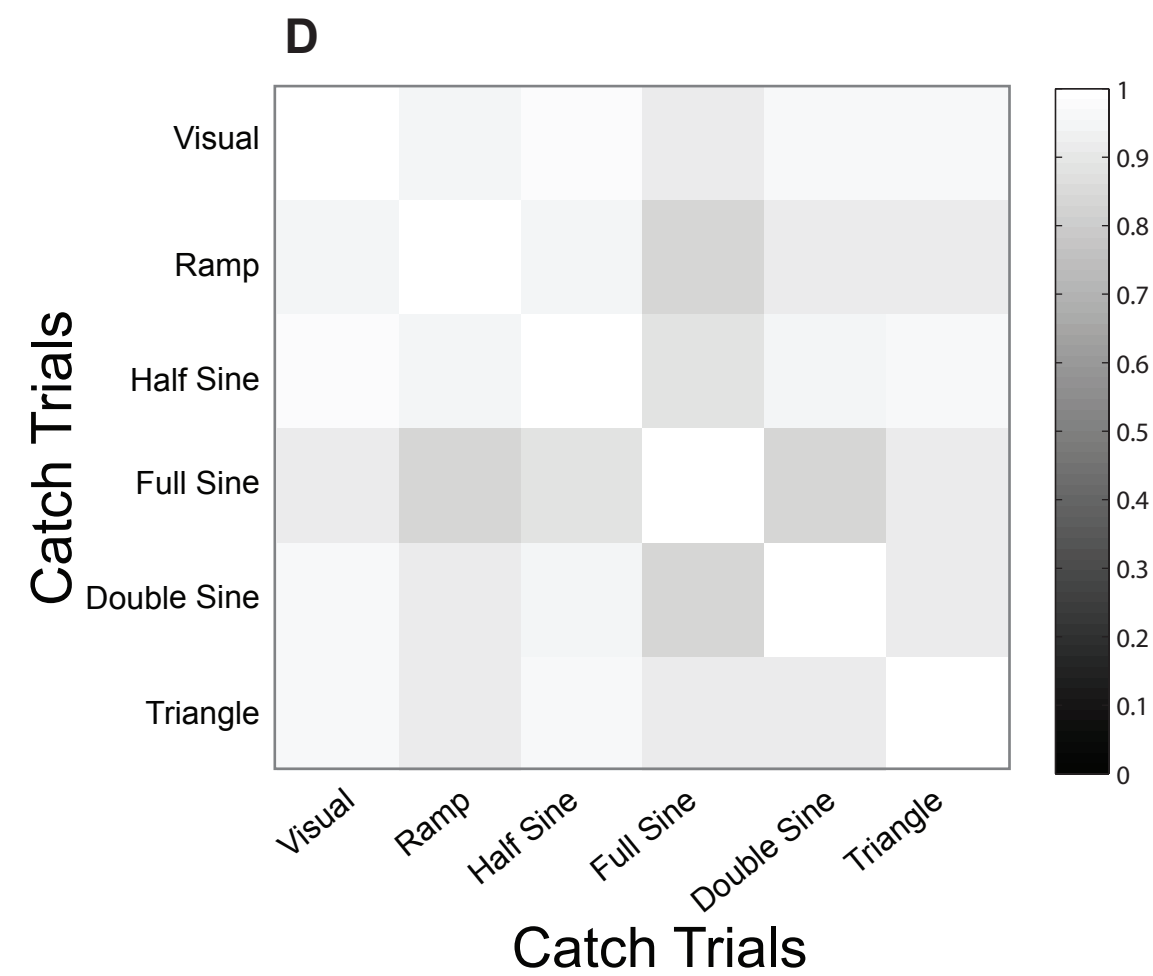
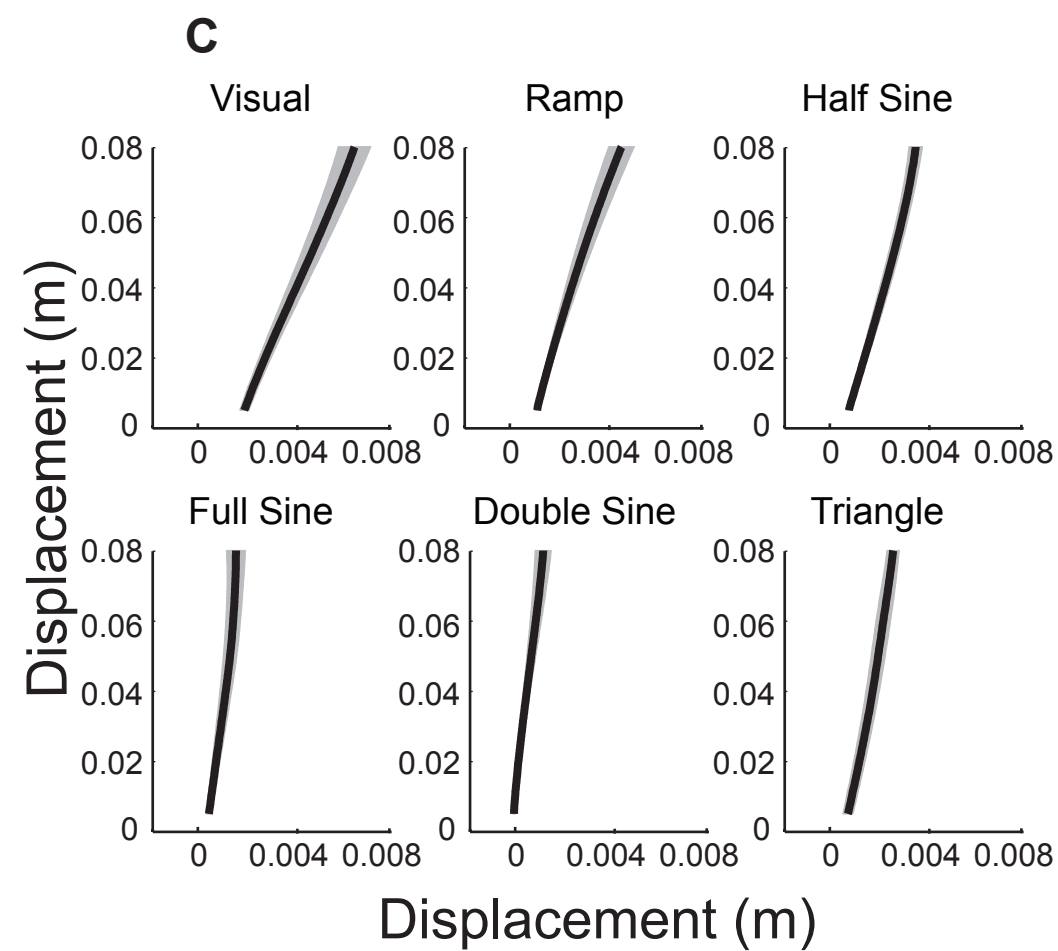
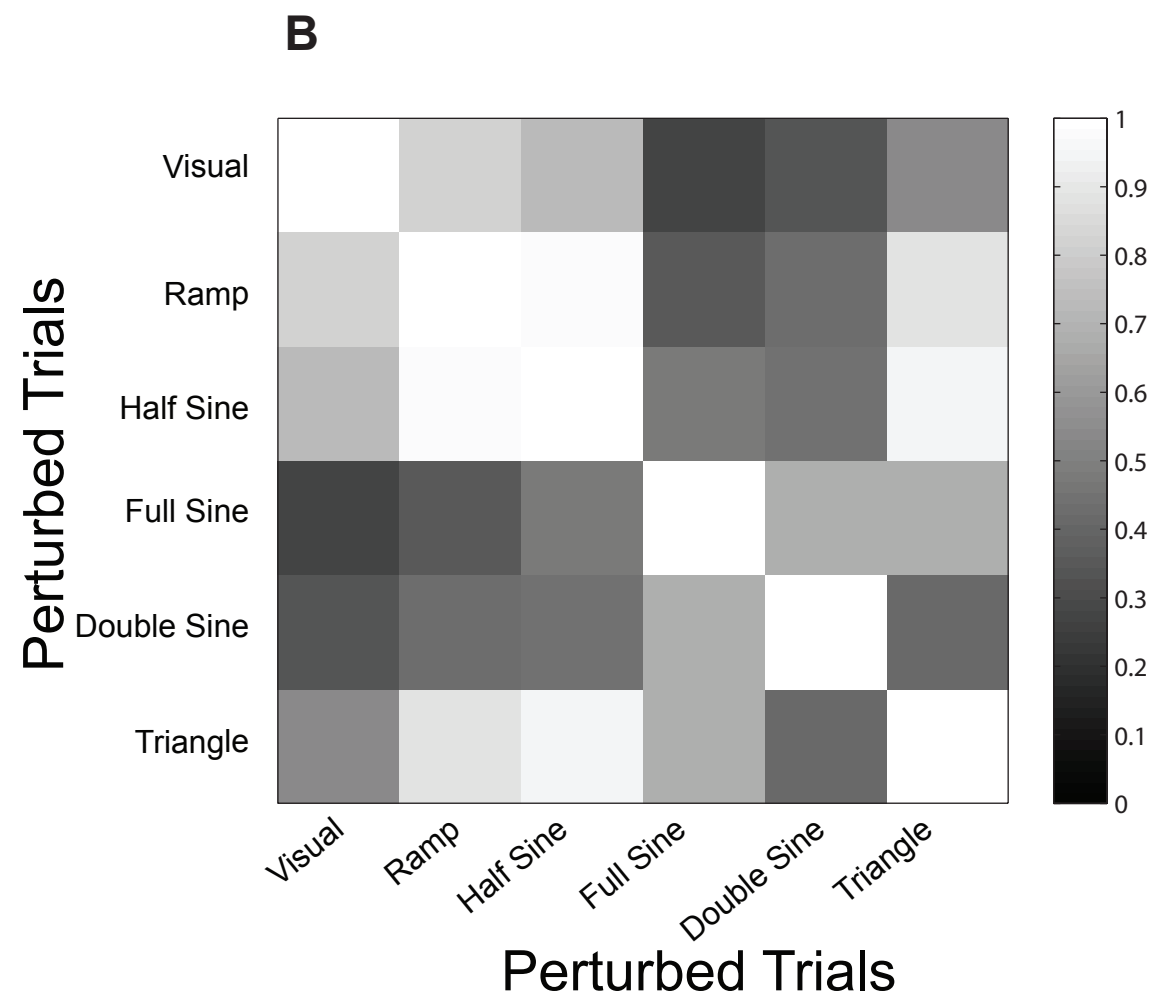
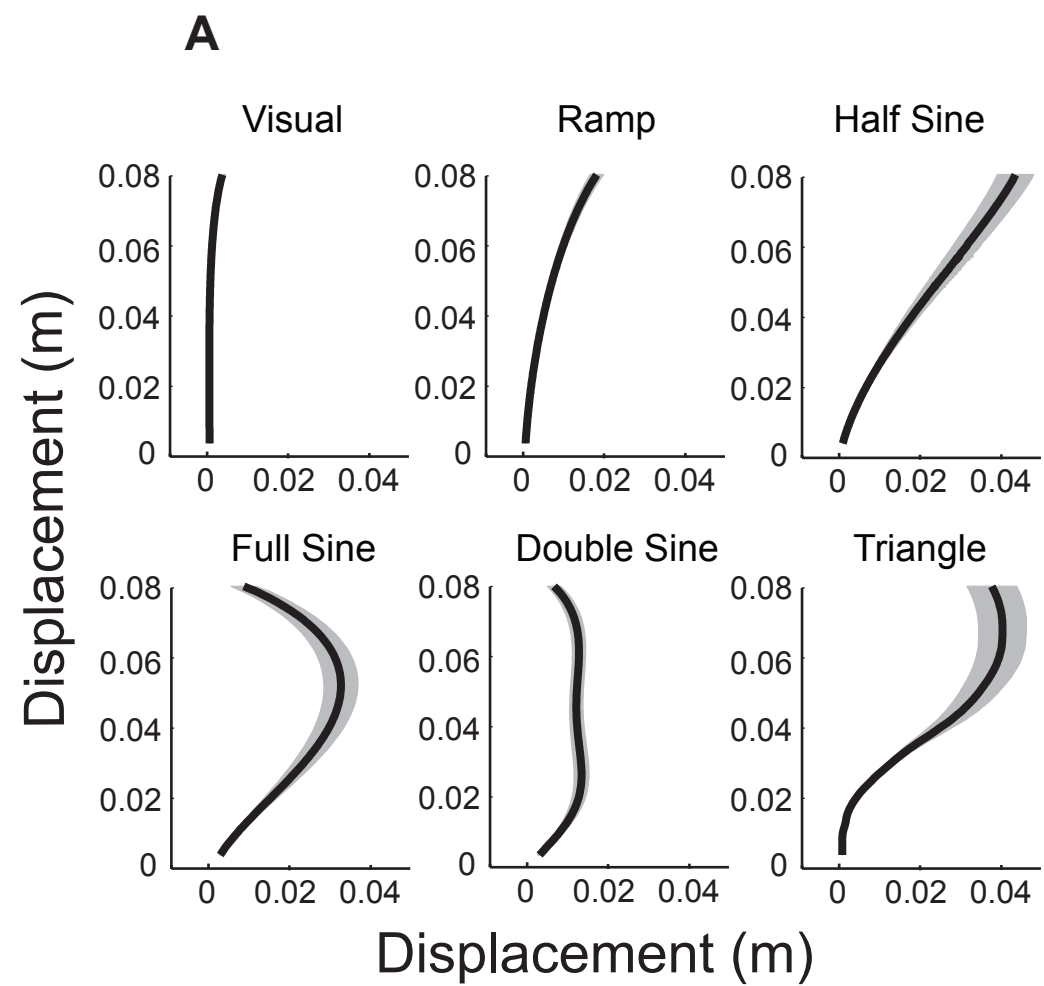
739 Figure 6: A-B). Correlation coefficients of pair-wise correlation between perturbation trials and
740 catch trials are displayed as grey shades for Experiment 1 and Experiment 2, respectively. The
741 correlation analysis is performed on acceleration trajectories for Experiment 1 and force
742 trajectories for Experiment 2. If the catch trial is specific to its preceding perturbation trial, the
743 largest correlation should be found for their pair-wise correlation, which lies on the diagonal
744 that is displayed as a grey dash line. The largest correlation and the second largest correlation
745 on each row are shown, most of which are not on the diagonal line. This suggests there is no
746 close correspondence between the perturbation and its corresponding catch trial. C). The
747 influence (α) of the perturbation trial onto corrective responses in the catch trial is plotted as a
748 function of conditions. None of the conditions has influence significantly different from zero
749 except the ramp condition for Experiment 1 and the triangle condition for Experiment 2. This
750 indicates that for most perturbations the first-trial adaptation is not specific.

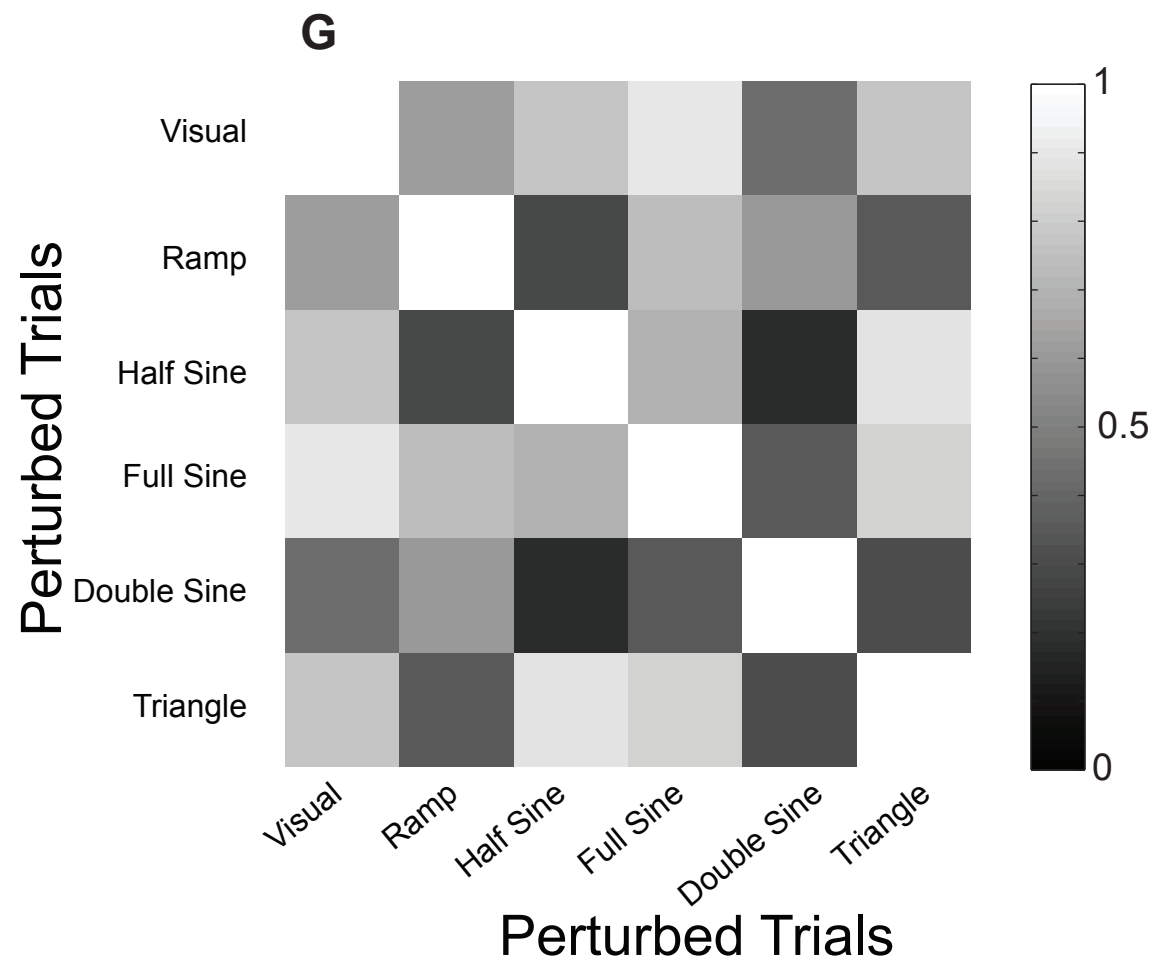
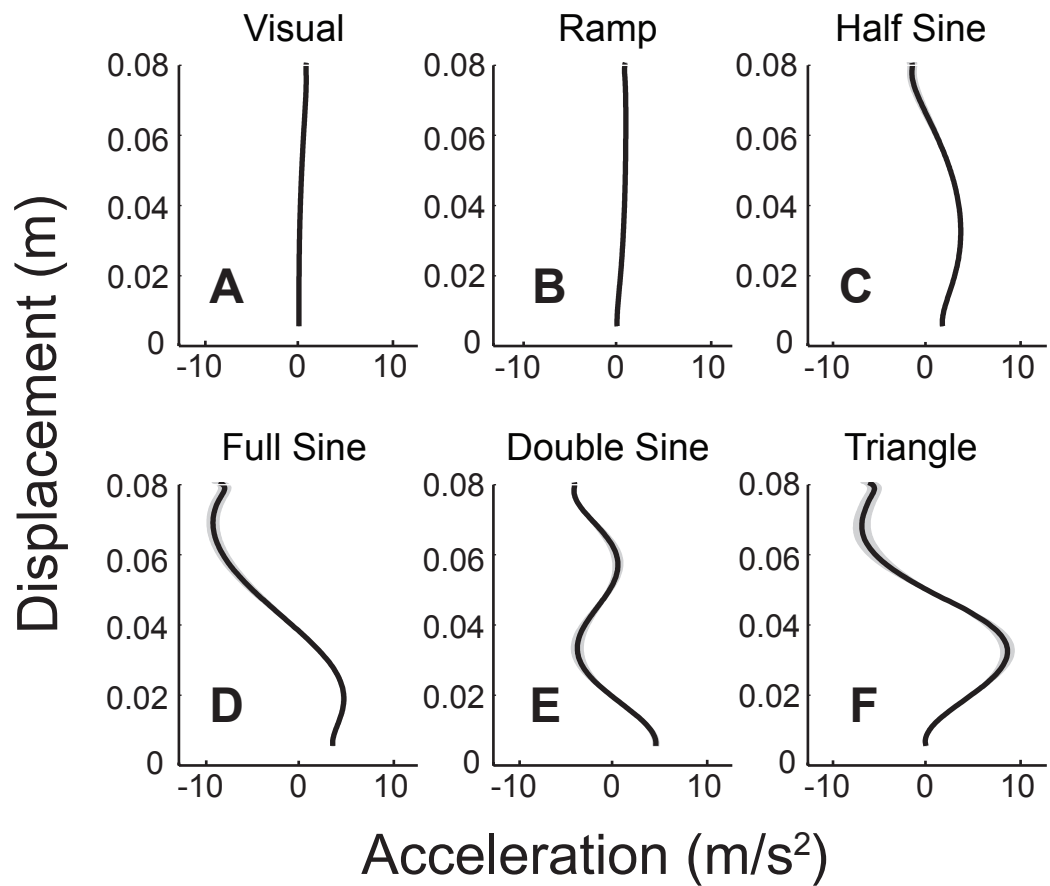
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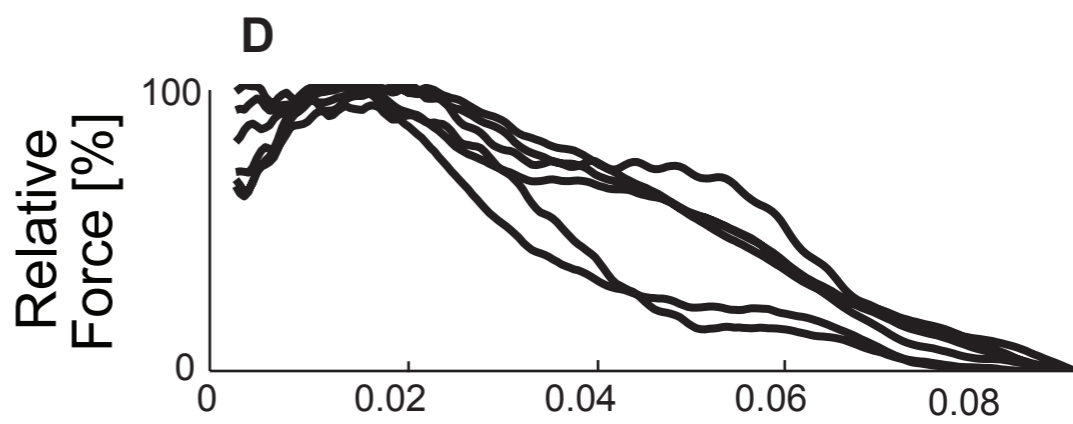
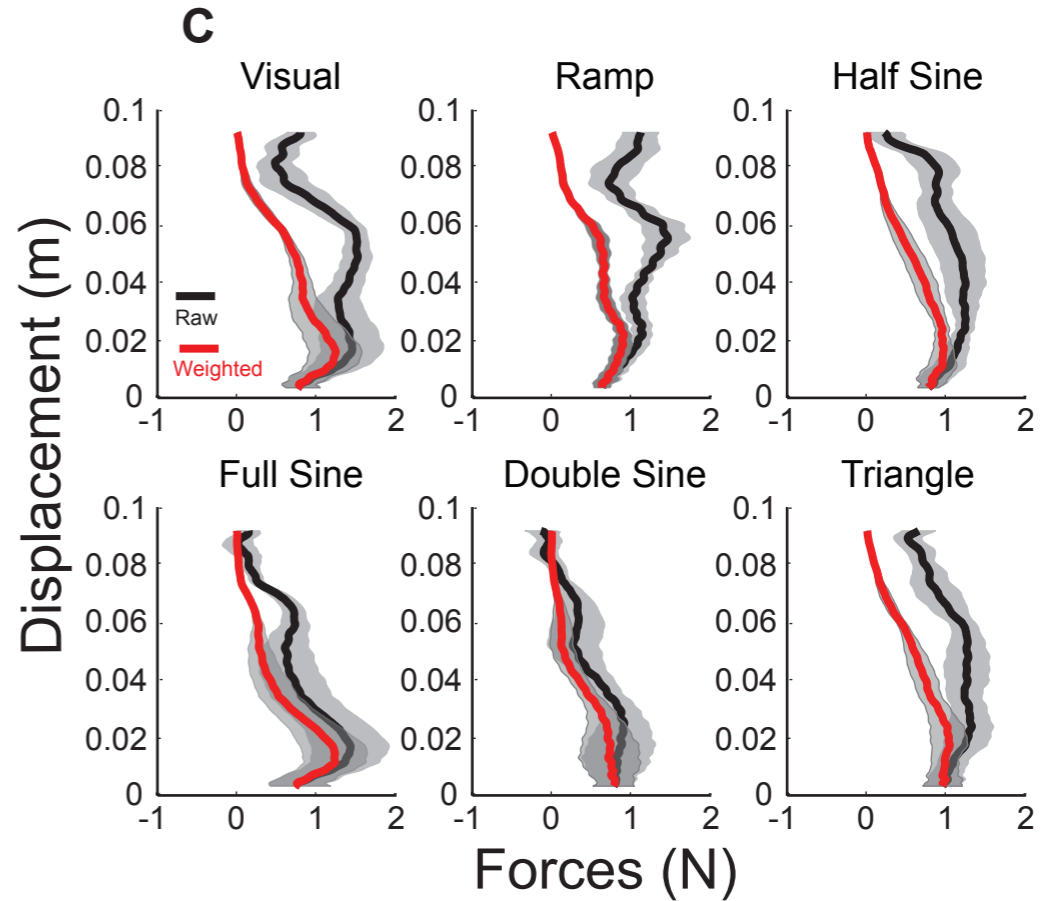
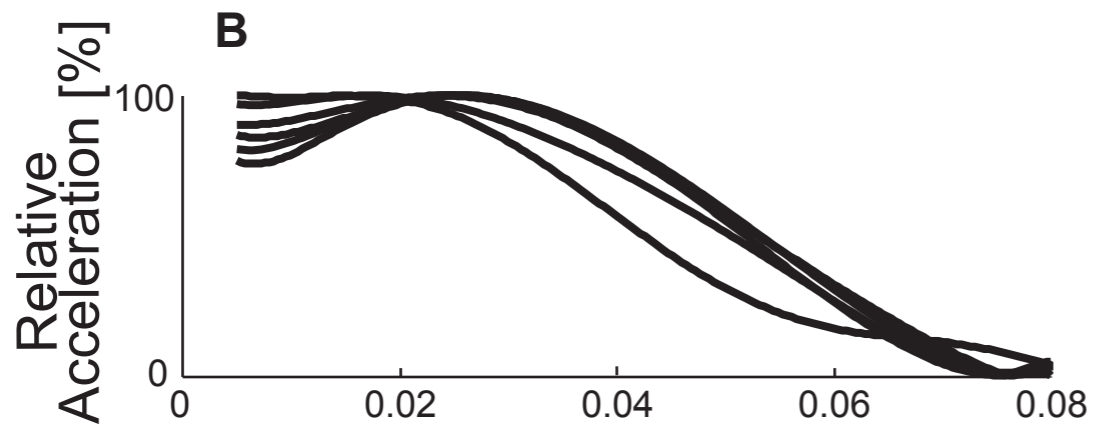
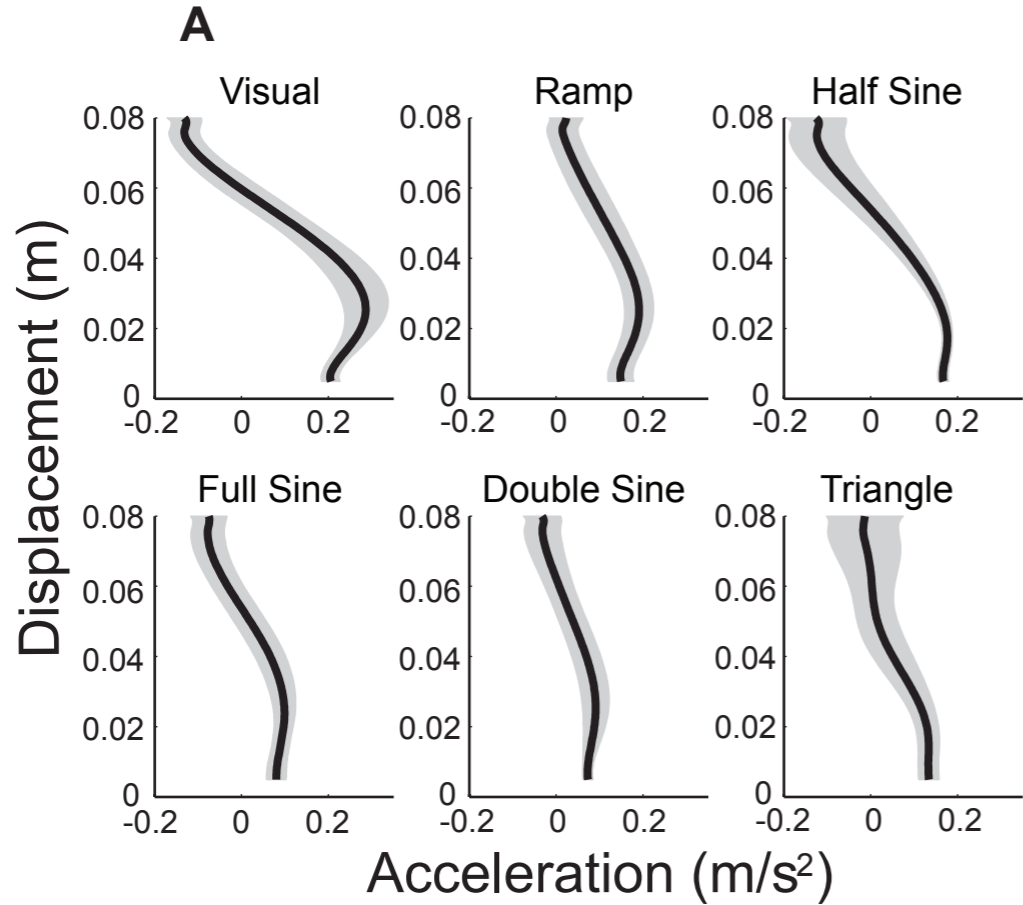
752 Figure 7: A-B). The first principal components of acceleration trajectories (panel A, Experiment
753 1) and force trajectories (panel B, Experiment 2) in catch trials are plotted against error
754 measures in its preceding perturbation trials. These error measures, shown by different subplots,
755 include the movement endpoint error, the maximal lateral deviation of the hand from the straight
756 path, the integral of the deviation over the movement, and the deviation at the peak velocity of
757 the reach, respectively. There is no visible dependence of between the trajectory and these error
758 metrics.



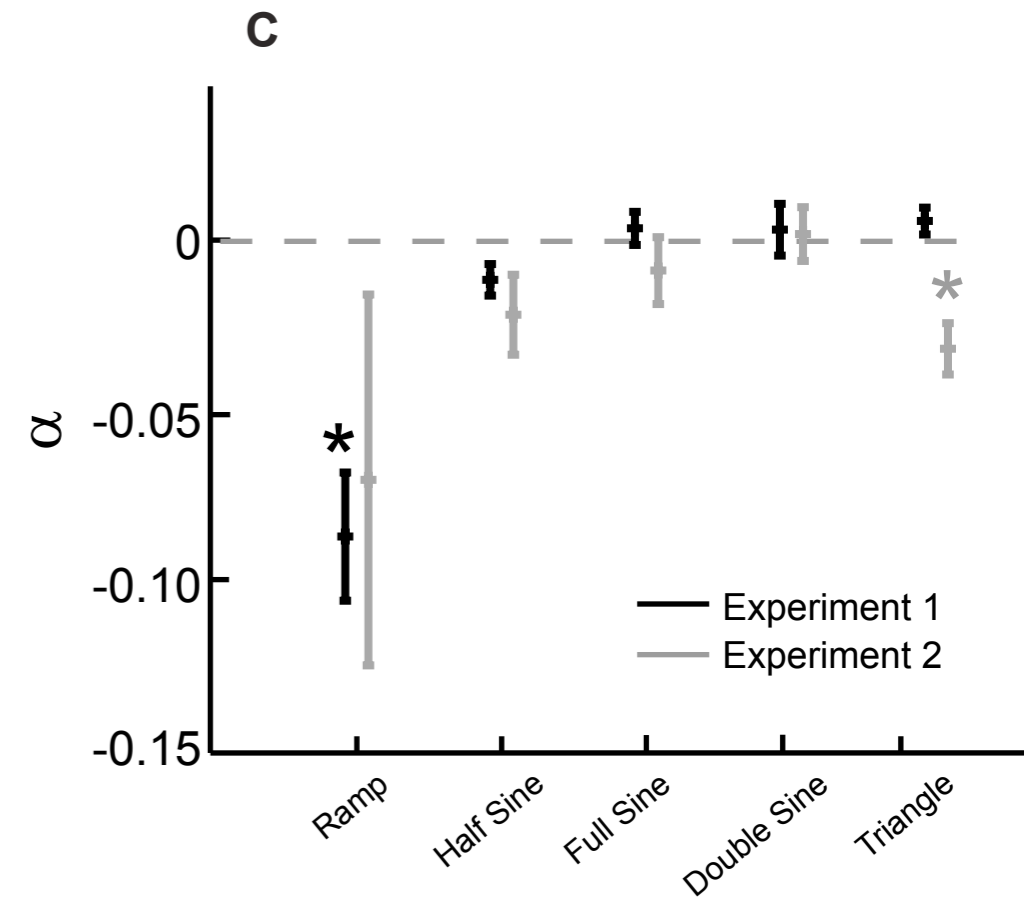
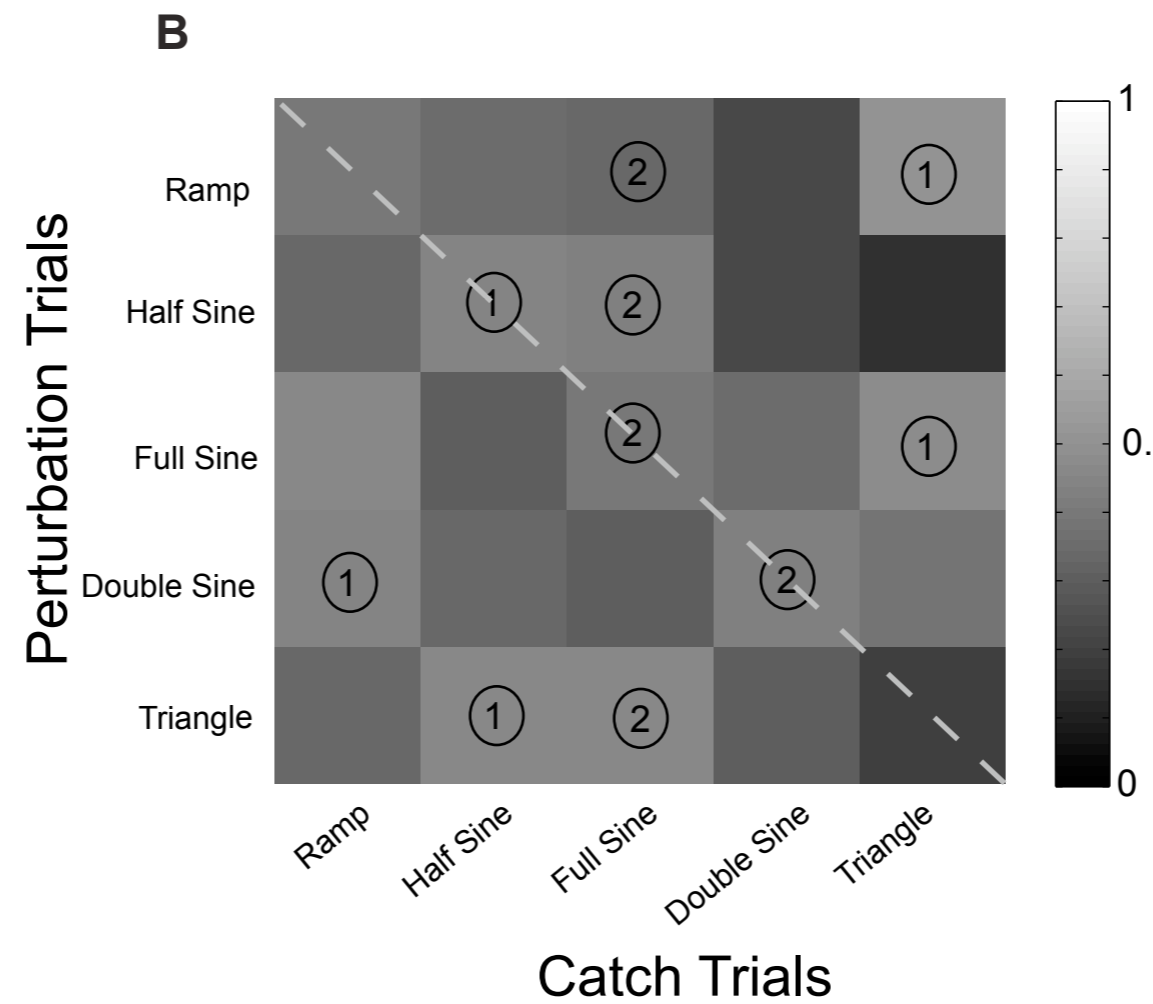
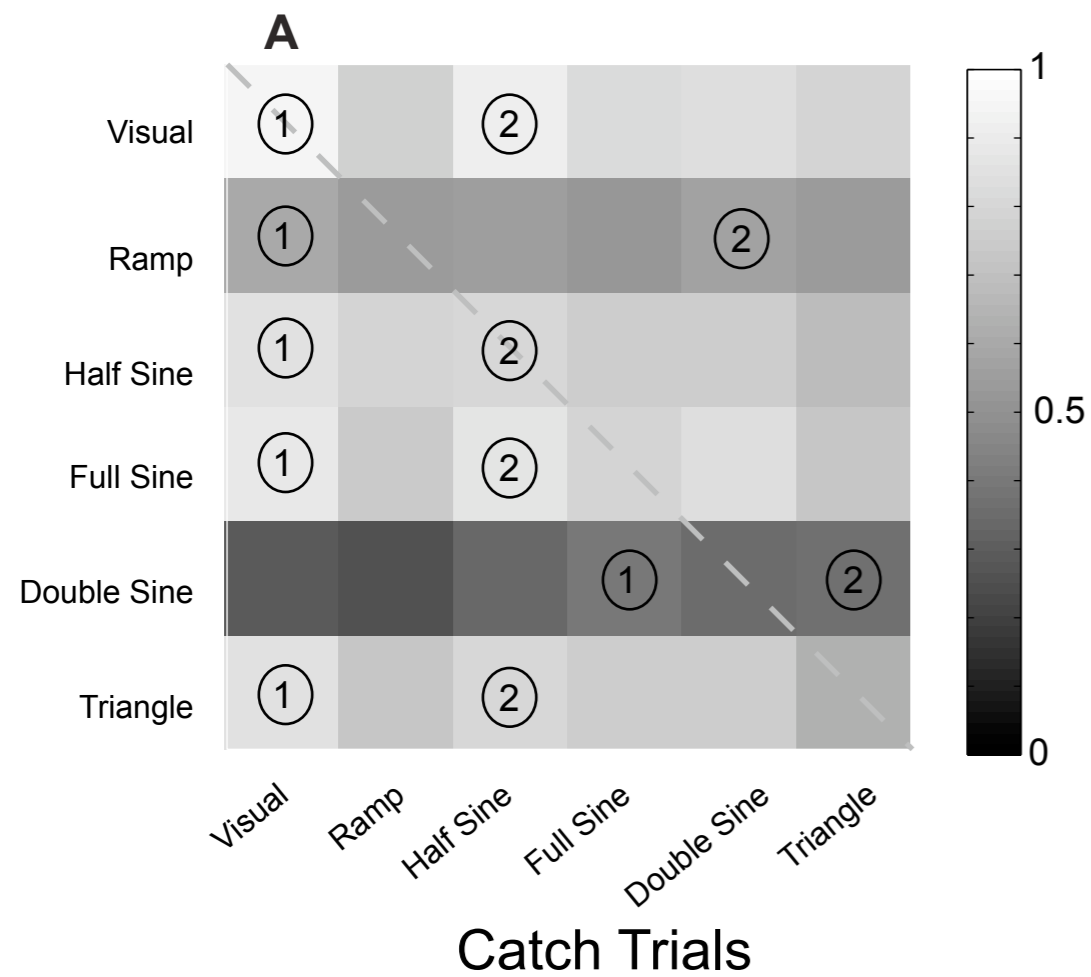




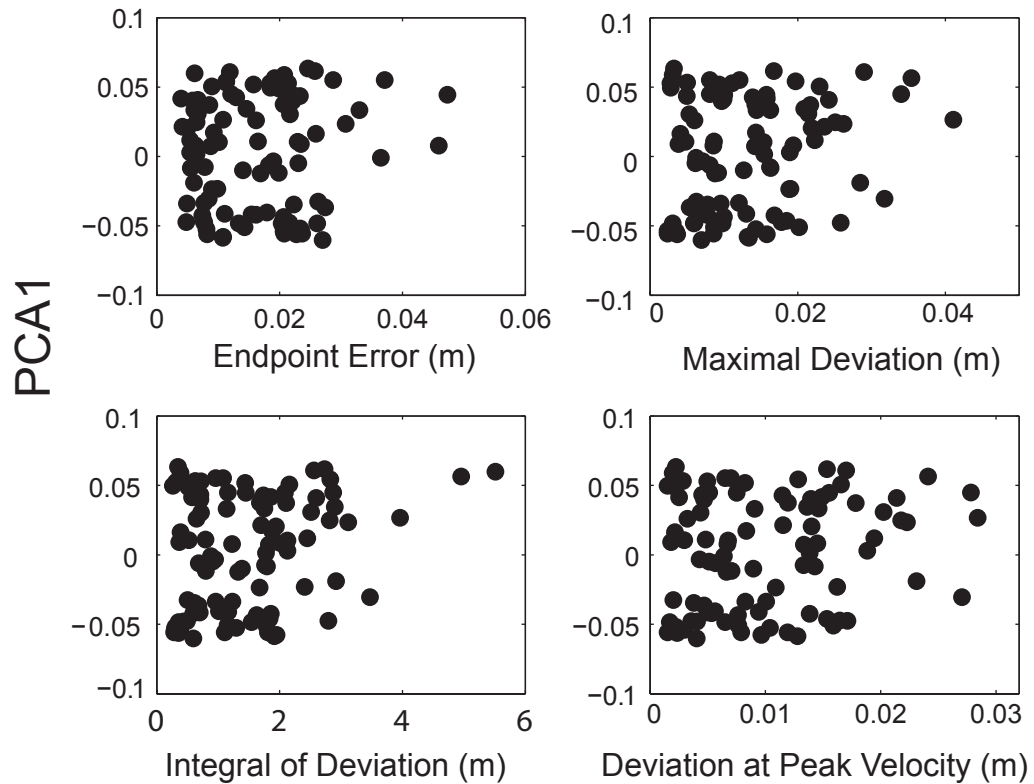




Perturbation Trials



A: Experiment 1



B: Experiment 2

