1   **A switching cost for motor planning**

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3   Running head: A switching cost for motor planning

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24

Abstract

Movement planning consists in choosing the intended endpoint of the movement and selecting the motor program that will bring the effector on the endpoint. It is widely accepted that movement endpoint is updated on a trial-by-trial basis with respect to the observed errors and that the motor program for a given movement follows the rules of optimal feedback control. Here, we show clear limitations of these theories. First, participants could not tune their motor program appropriately for each individual trial. This was true even when the participants selected the width of the target that they reached toward or when they had learned the appropriate motor program previously. These data are compatible with the existence of a switching cost for motor planning, which relates to the drop of performance due to an imposed switch of motor programs. This cost of switching shares many features of costs reported in cognitive task switching experiments and, when tested in the same participants, was correlated with it. Second, we found that randomly changing the width of a target over the course of a reaching experiment prevents the motor system from updating the endpoint of movements on the basis of the performance on the previous trial if the width of the target has changed. These results provide new insights into the process of motor planning and how it relates to optimal control theory and to an action selection based on the reward consequences of the motor program rather than based on the observed error.

New and Noteworthy:

Randomly changing the width of the target (random schedule) has a deep impact on the optimality of the reaching movements made by human participants, which suggests the existence of a switching cost for motor control. In addition, a change in target width made them unable to take into account the error observed on the previous trial to update their movement plan for the next trial. These results suggest new principles for movement planning.

Introduction

Movement planning, which includes all the processes occurring before the movement (detection and selection of target, selection of feedback control policy, etc.) is widely thought to follow two distinct rules. First, the control policy (how the brain will react with respect to incoming sensory input during the movement) is tuned according to optimal control laws (Todorov and Jordan, 2002; Shadmehr and Krakauer, 2008; Diedrichsen et al., 2009; Pruszynski and Scott, 2012). Second, movement performance is adjusted on a trial-by-trial basis via learning from errors even when learning or adaptation are not explicitly required (van Beers, 2009; Verstynen and Sabes, 2011; Dingwell et al., 2013; Wong and Shelhamer, 2014). In this paper, we demonstrate that these two rules are violated as soon as the target width changes randomly over the course of trials.

Such disruption of performance due to randomization is widespread in motor tasks (Elliott and Allard, 1985; Edin et al., 1992; Horak and Diener, 1994; Khan et al., 2002; Pruszynski et al., 2008; Selen et al., 2009; Bennett et al., 2010; Afsanepurak et al., 2012) (but see White and Diedrichsen, 2013). For instance, in a recent study (Orban de Xivry, 2013), we asked participants to reach to either a narrow or wide target and found that participants reacted differently to a perturbation as a function of the target width (compatible with the minimum intervention principle of optimal control, Todorov and Jordan, 2002) but unexpectedly also as a function of the schedule (random or blocked). That is, the modulation of the response to perturbations with target width was smaller in the random (target width randomly changes from trial-to-trial) than in the blocked schedule. The behavior in the blocked schedule was optimal because it minimized energy while maximizing reward.

Similar decrease in performance due to randomization is also observed in cognitive tasks where it falls in the category of switching costs under the name of mixing cost (i.e. the long-term cost of task switching). A switching cost relates to the inability of the participants to switch from one task to another without a penalty in behavior (Monsell, 2003; Kiesel et al., 2010). Typically, in cognitive studies, this cost is reflected in an increase in reaction time (Allport et al., 1994; Rogers and Monsell, 1995). For instance, when participants are required to report the color or the shape of a symbol based on some abstract rules, the reaction time is shorter when the rule is presented in blocked schedule (i.e. the rule remains unchanged for several trials in a row) than when the rule can change randomly from trial-to-trial. Such switching cost is also present when participants choose the rule that they want to apply on each trial (Arrington and Logan, 2004, 2005).

While in the previous paper (Orban de Xivry, 2013), we merely reported the observation that randomly changing the width of the target affected the optimality of motor behavior, we present in this paper three

experiments that provide an explanation for the absence of optimality in the random schedule and identify limits on the flexibility of motor planning. Importantly, in this study, like in many others (Ahmadi-Pajouh et al., 2012; Nashed et al., 2012; Dimitriou et al., 2013; Orban de Xivry, 2013; White and Diedrichsen, 2013), we consider that motor planning (i.e. before movement onset) consists in the derivation of a goal-directed feedback control law (Todorov and Jordan, 2002; Scott, 2004; Todorov, 2004; Liu and Todorov, 2007) and that responses to any perturbations during the movement are driven by this feedback law. Thus, these perturbations at any time during movement allow us to probe the feedback control policy determined before movement (Liu and Todorov, 2007; Nashed et al., 2012; Gallivan et al., 2016).

Each of these three experiments represents a critical test of the hypothesis that the absence of optimality in the random schedule is due to a switching cost and that this switching cost shares similarities with the one observed in cognitive tasks. In the first experiment, we test whether voluntary selection of target width can improve switching behavior knowing that it does not in cognitive switching tasks. Such failure to optimize the control policy under voluntary selection of target width would confirm that the difference between the random and blocked schedules was not related to the imposed target selection and to a too short time for movement planning. The second experiment aims at testing whether the difference between the random and blocked schedules was due to the ignorance of the optimal motor behavior during the random schedule as it was always tested first. The third experiment investigates the limit in trial-to-trial switches in order to confirm the inability to fully modify the motor program from one trial to the other. A failure of any of these experimental manipulations would cast doubt on the existence of a switching cost for motor control and would favor other alternative accounts for the observed differences between the random and blocked schedules. In contrast, confirmation of such as switching cost would provide new insights into the mechanisms of motor planning (Cisek and Kalaska, 2010; Wong et al., 2015).

Methods

Participants

Sixty-one healthy participants (21 for experiment 1 and 20 for experiment 2 and 3) were enrolled for the experiments after written informed consent. All participants had no history of neurological disorders, were right-handed and between 18 to 40 years old. All procedures were approved by the Ethics Committee of the Université catholique de Louvain. We also analyzed some new aspects of the data from the 50 participants from our previous paper (Orban de Xivry, 2013).

Setup

Participants were sitting in front of a robotic arm (Endpoint Kinarm, BKin Technologies, Kingston, Ontario, Canada) that controlled a cursor that appeared to be positioned at the same position in space as the hand through a mirror setting. Participants could not see their hand and the displayed cursor was the only available visual feedback of their hand position. Hand position, velocity and acceleration and the force exerted by the participants on the handle of the robot were recorded at 1000Hz and stored on a computer for offline analysis. The robot was also able to exert forces in order to perturb or direct the hand of the participants.

Protocol

Cognitive task switching

In this cognitive task switching, participants had to indicate either the color or the shape (depending on a specific instruction) of a symbol by applying a force with their right or left hand (Fig.1, cognitive task switching). Depending on the schedule, the instruction varied randomly from trial-to-trial or remained unchanged for several trials in a row. More specifically, participants had to respond to the appearance of a visual stimulus (disk (radius: 1cm, surface: $3.14cm^2$) or square ($1.75 \times 1.75cm$, surface: $3.06cm^2$) that was either blue or orange (these colors were colorblind-friendly) on the screen of the Kinarm setup by applying an isometric force of 7N on the left or right arm of the robot (bimanual task) following one of two possible rules. The direction of the force was irrelevant, only its magnitude was taken into account. For the shape rule, participants had to indicate whether the shape was a square or a circle. The association between shape and hand of the response was counterbalanced across participants. For the color rule, the participants had to indicate whether the symbol was orange or blue. The association between color and hand of response was counterbalanced across participants. On each trial, the relevant rule was indicated by a solid white line (20cm wide) that was displayed 1.5cm above the symbol for the shape rule and 1.5cm below the symbol for the color rule. When a participant made a mistake, a red line (20cm wide) appeared on top of the symbol. Intertrial time interval was 400ms. Participants had maximum 5s to provide their response.

After one to three blocks of training to demonstrate the task (20 trials each), the participants performed three blocks of trials. In the random schedule (first and third blocks, 40 and 64 trials), the rule (indicate shape or indicate color) could change pseudorandomly from trial to trial. In this schedule, every mini-block of 8 trials contained all 8 possible combinations of shape, color and rule. Within each mini-block, the order of the eight different trials was fully randomized. The first and last block contained respectively

5 and 8 mini-blocks. In contrast, during the second block, the rule remained unchanged for the first half of

142 the block (20 trials) after which it switched to the other rule until the end of the block (20 trials).

A - Cognitive task switching

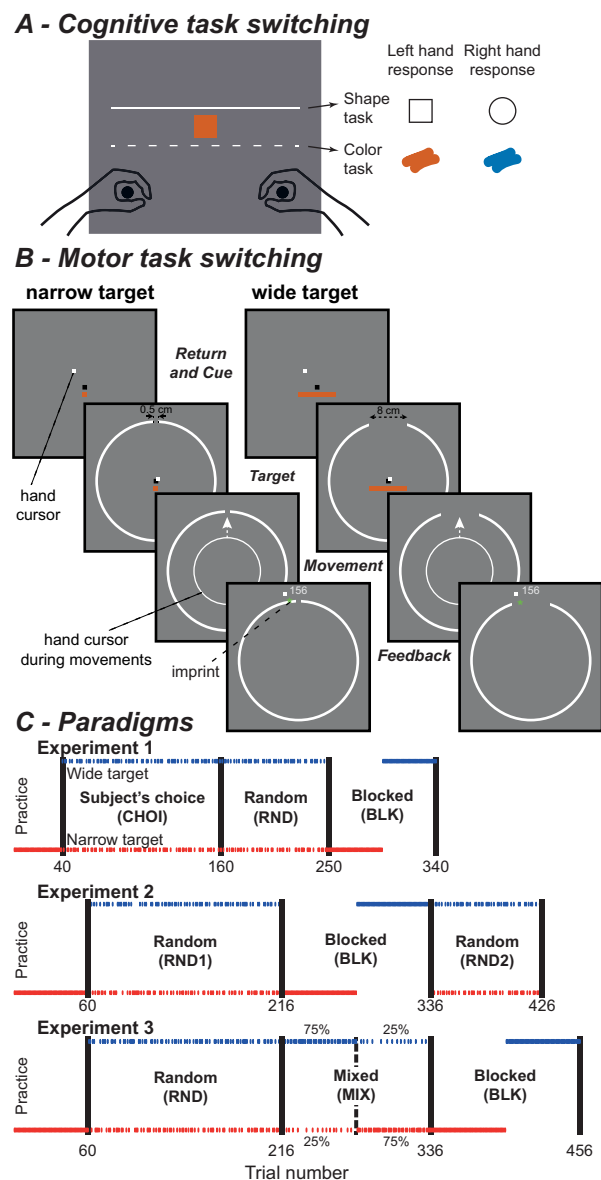**B - Motor task switching**

C - Paradigms

143

144 Figure 1: Experimental protocols. A) Cognitive task switching: participants had to indicate the shape
145 of the symbol (shape task: square or circle) if a white line was displayed above the symbol on the
146 screen (as on the panel) or its color (color task: orange or blue) if the line was below it (at the place of
147 the dashed line). The response was indicated by exerting an isometric force on the left or right handle
148 of the robot manipulandum. The situation depicted on the figure requires a left hand response. The
149 hands were not visible for the participants. B) Motor task switching: In this task, participants were
150 instructed to bring the cursor through the aperture of a circle. This aperture was always at the same
151 location but could have one of two possible widths (0.8 or 8cm). Each trial started with the appearance
152 of the starting position (Black square, return and cue phase). During this phase, a cue indicated the
153 width of the aperture for the ensuing trial (orange symbol, Return and Cue phase). The target was then
154 presented 15 cm away from the starting position in front of the participant (Target phase). When the
155 participants initiated their reach, the hand cursor was replaced by a circle whose radius increased with

156 the distance travelled by the hand (Movement phase). Veridical hand position was provided after
157 movement end in order to provide feedback about movement accuracy (feedback phase). Additional
158 information was provided via the imprint that the hand left on the circle when it crossed it. The imprint
159 was blue if movement duration was too long, yellow if movement duration was too short and green if
160 movement duration was between 500 and 600ms. One point could be earned for good movement speed
161 and another point could be earned for good accuracy. The total number of points collected so far
162 during the block was displayed at the end of each trial (156 points in the illustration). C) The three
163 panels illustrate the repartition of trials with the narrow and wide target over the course of the three
164 experiments (see main text). The y-axis represents target width and the x-axis trial number. In the
165 CHOI schedule, participants selected the width of the target for each trial and were instructed to do so
166 randomly. In the random schedule, target width was randomly varied from trial-to-trial. In the blocked
167 schedule, target width remained unchanged for either 45 trials (experiment 1) or 60 trials (experiments
168 2 and 3). The order of target width was counterbalanced across participants. In the MIX schedule, there
169 was an imbalance in the percentage of trials for each target width (75% - high probability trials vs 25%
170 - low probability trials). Each participant received 60 trials with higher probability of one target width
171 followed by another series of 6o trials where the other target width was more frequent. The order was
172 also counterbalanced across participants.

Motor task switching

174 Participants were instructed to shoot through a target whose width could vary from trial-to-trial. The target

175 consisted of an aperture within a white circle (radius: 15cm), which was always centered on the starting

176 position (25mm^2 red square located 15cm in front of the participant's chest). The width of the aperture

177 could be either 0.8cm or 8cm (Fig.1, target phase). The width of the target on the next trial was presented

178 well in advance of target presentation (Fig.1, cue phase). An orange 0.8cm square or a 0.8cm x 8cm

179 rectangle was provided as a cue in order to indicate the width of the aperture for the upcoming movement.

180 This cue was presented 3mm below the starting position and at the same time as the starting position (~1s

181 before reach onset). This cue disappeared at reach onset. The circle that delimited the target appeared after

182 a delay between 700 and 850ms once the hand of the participant was stabilized inside the starting position

183 and, in the CHOI schedule, after the participant had made his/her choice about the width of the target (see

184 below). Once the target had appeared, participants had to reach through the target in a given time interval

185 (500-600ms, movement phase in Fig.1) without any information about the direction of their movement

186 (see below). As soon as the hand crossed the circle, it left an imprint in order to provide accurate feedback

187 about the accuracy of the movement (Fig.1, feedback phase). The color of this imprint provided feedback

188 about the speed of the movement (blue=too slow, yellow=too fast, green=good speed). When movement

189 duration was between 500 and 600ms, participants earned one point. They also earned an additional point

190 if the imprint was within the aperture.

191 Movement onset and offset were detected online with position and velocity criteria. Movement onset was

192 flagged when the hand left the area of the starting position and hand velocity was higher than 0.02m/s.

193 Movement end was detected when the distance travelled was larger than 15cm. A few hundreds of

194 milliseconds after movement end, the hand was pushed back towards the starting position while the hand

195 cursor was removed from the screen.

The experiment was divided into blocks of trials that were separated by a one-minute break. All participants started the experiment with a practice block. During this block, they performed tens of movements (40 trials in experiment 1, 60 trials in experiments 2 and 3) towards the 0.8 cm aperture with a small hand cursor (cursor was 9mm^2) that provided online visual feedback of hand position to the participants. This block aimed at training participants to reach to the target at the good speed. After the practice block and for the rest of the experiment, a modified hand cursor was used during the movements towards the target (Movement phase, Fig.1). This cursor was an expanding circle that indicated the distance traveled by the hand but not the direction taken by the participant. Outside the movement period, the hand cursor was a 9mm^2 square. When the hand exited the circle, the small cursor indicated again the actual position of the hand. An imprint that was located on the circle indicated exactly where the hand of the participants crossed the boundary of the circles in order to provide accurate endpoint performance.

For 20% of the trials of all experimental blocks (i.e. not during the practice blocks), the hand path was constrained by stiff virtual walls (perturbation trials). These walls (Scheidt et al., 2000) were created by applying a stiff unidimensional spring (spring stiffness: 2500 N/m and viscosity: 25 Ns/m) and acted as a mechanical guide that directed the hand towards the center of the target or 2cm either on the left or the right of it. The lateral deviation observed during these trials was less than 0.5 mm In these trials, the actual position of the hand was concealed to the participant by 1) using the circular feedback during the movements 2) displaying the feedback imprint at the center of the target when the subjects crossed the target and 3) showing the projection of the actual position of the hand on the midline rather than its actual position once the hand exited the circle. To make sure that our results were not influence by this fake feedback, we removed all the trials immediately following a perturbation trial from all analyses. These trials were randomly interspersed throughout the experimental blocks.

In experiment 1, we tested the ability of the participants to voluntarily modulate their behavior when they themselves select the target width. This experiment started with a block of at least 120 trials during which participants selected the width of the target on each trial (CHOI schedule). The actual number of trials in this first block varied from participant to participant as the block was stopped only once the participant had chosen 60 times each of the two targets. Before the appearance of the starting position, participants indicated orally to the experimenter the width of the target that they would like to receive on the next trial. The operator then selected the correct target size for the upcoming movement. This first block was followed by two blocks of 90 trials each. In the first block (RND schedule), target width was varied pseudo-randomly (the order of trials was prearranged before the experiment). In the second block (BLK schedule), half of the participants experienced the narrow target for 45 trials followed by another 45 trials

228 with the wide target. The order of target width was counterbalanced for the other half of the participants.
229 In summary, experiment 1 consisted of three different schedules: CHOI, RND and BLK.

230 In experiment 2, we tested the ability of the participant to form a memory of the optimal behavior
231 exhibited during the BLK schedule in a later random schedule. In this experiment, during the first and
232 second experimental blocks (66 and 90 trials, random schedule, RND1), the target width was varied
233 randomly (i.e., for block 2, the order of trials was prearranged before the experiment,) from trial to trial.
234 During the third one (blocked schedule, BLK), half of the participants experienced the narrow target for
235 60 trials followed by another 60 trials with the wide target. This order was counterbalanced for the other
236 half of the participants. During the fourth block (RND2, 120 trials), the width of the target was again
237 pseudo-randomly presented from trial to trial. In summary, experiment 2 consisted of three schedules:
238 RND1, BLK and RND2.

239 In experiment 3, we tested the ability of the participants to update their motor program from one trial to
240 the next. This experiment consisted of four different blocks. During the first and second experimental
241 blocks (66 and 90 trials, random schedule, RND), the target width was varied randomly from trial to trial.
242 During the third one (Fig.1C, mixed schedule, MIX), half of the participants experienced 60 trials where
243 the narrow target was presented in 75% of the trials (high probability trials) and the other 25% (low
244 probability trials) were randomly interspersed trials with the wide target. These 60 trials were followed by
245 another 60 trials with high probability trials with the wide target (75% of the trials) and low probability
246 trials with the narrow target). The order of target width associated with high-probability trials was
247 counterbalanced for the other half of the participants. In other words, all the participants experienced high
248 and low probability trials with both the narrow and wide targets. Importantly, 8 of the 15 low probability
249 trials were perturbation trials. During the fourth experiment block (BLK), the width of the target was
250 blocked. In summary, experiment 3 consisted of three schedules: RND, MIX and BLK.

Data analysis

252 In perturbation trials, we used the signed lateral force exerted by the participants against the wall of the
253 channel as a proxy of their willingness to go towards the center of the target. Force measures were low-
254 pass filtered (second order Butterworth filter with cutoff: 75Hz). The average lateral force from straight
255 ahead perturbation trials was subtracted from the measures of lateral force during rightward or leftward
256 perturbation trials separately for each schedule and target width separately. These corrected measures
257 were sign reversed for the rightward perturbations such that a larger positive force represents a larger
258 reaction to the perturbation. To quantify the reaction to the perturbation, we extracted the lateral force
259 exerted by the participants when they were 2cm away from the target. These 2cm allowed us to avoid late

260   correction of the movements or the period where the cursor was back to normal size. To assess the effect

261   of time on this variable, the same measure was also taken at 7cm from the starting position (~240ms into

262   the movement).

263   In unperturbed trials, our proxy for movement performance was the lateral position of the hand when it

264   was 2cm away from the target. This measure was considered as movement endpoint. This measure of

265   movement endpoint was highly correlated with the movement endpoint when the hand crossed the target

266   ($R>0.8$) but had the advantage to contain many more points. Indeed, on some trials, participants stopped

267   their movement before reaching the target (percentage of such movement varies between participants and

268   experiments but is smaller than 0.25% of the trials). In such case, the value at 15cm cannot be computed.

269   Unperturbed trials were excluded from these analyses if they immediately followed a perturbed trial. To

270   assess how the performance of one trial affected the performance on the next trial, we computed lag 1

271   autocorrelation of endpoint errors between pairs of trials. Note that pairs of consecutive trials that include

272   a perturbation trial were also excluded from this analysis. The autocorrelation function was computed for

273   each subject individually and the values of the auto-correlation were then averaged across subjects.

274   In experiment 1: ANOVA was used with schedule (CHOI, RND, BLK) and target width (narrow and

275   wide) as within-subjects factors.

276   In experiment 2: ANOVA was used with schedule (RND1, BLK, RND2) and target width (narrow and

277   wide) as within-subjects factors.

278   In experiment 3: ANOVA was used with schedule (RND, MIX-high probability, MIX-low probability,

279   BLK) and target width (narrow and wide) as within-subjects factors. The factor MIX-high corresponded to

280   the 75% of trials that had the same target width while the factor MIX-low represented the remaining 25%.

281   In the cognitive task switching experiment, the reaction time was taken as the time between the

282   appearance of the symbol on the screen and the force magnitude (in any direction) reached a threshold of

283   6N (which required a strong response from the participant). Then we computed the median reaction time

284   of the correct trials for each epoch separately.

285   To assess how much the performance on one trial was taken into account in the next trial, we followed the

286   method proposed by Van Beers (van Beers, 2009; van Beers et al., 2013a, 2013b). Van Beers showed that

287   when errors are taken into account, the correlation between errors on consecutive trials is low because the

288   trial-to-trial error correction mechanisms should reduce the relationship between the movement directions

289   from one trial to the other. In contrast, when error correction mechanisms are absent, the relationship

290   between the planned directions of two consecutive trials is only disrupted by noise as it looks like a

291 random walk. Therefore, the correlation of endpoint error between pairs of consecutive trials is much

292 higher when error correction mechanisms are absent than when they are present. Further justification for

293 this analysis can be found in Van Beers et al. (2013a). To assess this correlation, we took into account all

294 the pairs of consecutive trials that did not contain a perturbation trial. For each of these pairs, we

295 considered the lateral position of the hand shortly before reaching the target (see above). Then we

296 computed the correlation coefficient between the lateral positions in these pairs of trials.

297 In order to take into account the different levels of force observed in the different experiments (e.g. due to

298 reaching or shooting), the analysis of the switching cost across the experiments from this paper and from

299 the previous one (Orban de Xivry, 2013) was carried on the normalized lateral force obtained by dividing

300 the lateral force by the average force.

Results

Self-selection of target width does not alleviate the inability to switch between two different control policies

304 In the first experiment, participants were asked to randomly select the width of the target before each trial

305 (CHOI schedule) in order to test whether self-selection of target width would allow the participants to

306 optimize their reaching movements on a trial-to-trial basis during a random schedule. This block was then

307 followed by two other blocks. In the first one, the target width was randomly changed from trial-to-trial

308 (random schedule, RND) while in the second, the target width remained constant for 60 trials before

309 switching to the other target width (block schedule, BLK). In each of these three schedules, we analyzed

310 how participants responded to perturbations during their movements as a function of the target width. By

311 doing so, we make the assumption that participants would use the same control policy in perturbed and

312 unperturbed trials because the perturbation trials were unpredictable and that the response to the

313 perturbation reflects the control policy that is used in unperturbed trials. Most of the participants did not

314 actually realize that in some trials, their hand was perturbed away from its trajectory.

315 Both in the CHOI and RND schedules, participants slightly modulated the force that they exerted against

316 the perturbation with target width. However, the modulation of the force with target width was

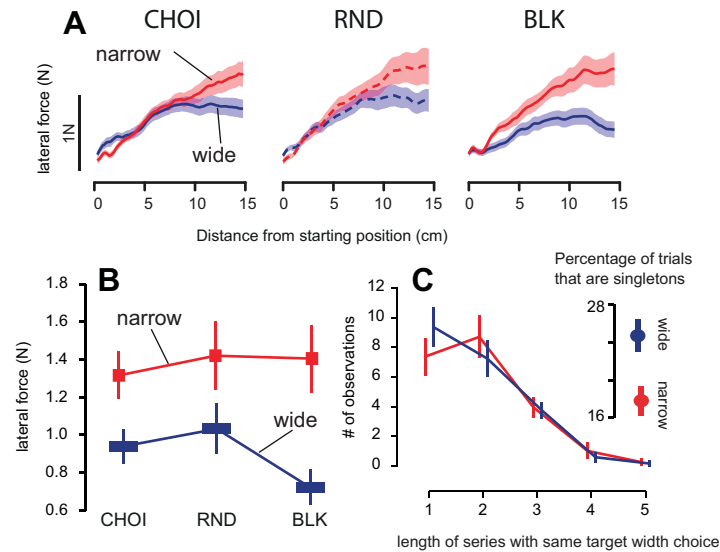317 significantly smaller than what was observed in the BLK schedule.

Figure 2: Self-selection of target width does not improve the ability to switch between two motor behaviors in comparison with the random schedule. A) Average force profiles across all participants recorded during the perturbation trials for each schedule (CHOI: self-selection of target width; RND: random schedule; BLK: blocked schedule) and each target width separately (red: narrow target; blue: wide target). In these plots, the forces are represented against the distance from the starting position in order to match the level of perturbation. Shaded area around each curve represents standard error of the mean. B) Average force (N) recorded at 13 cm in the force profiles as a function of target width and schedule. Error bars are standard error of the mean. C) Average distribution of the length of series of trials with the same target width (i.e. how many trials in a row had the same target width). Error bars are standard error of the mean. Inset in panel C) Proportion of trials where the target width is different from the target width on the previous and next trials.

This observation was confirmed by a repeated-measure ANOVA with schedule (CHOI, RND and BLK) and target width (narrow or wide) as within-subject factors. The ANOVA yielded an interaction between target width and schedule ($F(2,40)=6.9$, $p=0.0026$). Further inspection of this interaction revealed that the difference in force for the narrow and wide targets (ΔF) was larger in the BLK schedule than in the two other schedules (paired t-test: ΔF_{BLK} vs ΔF_{CHOI}: $t(20)=-3.12$, $p=0.005$; ΔF_{BLK} vs ΔF_{RND}: $t(20)=-3.04$, $p=0.006$). There was no statistical difference in ΔF between the CHOI and RND schedules ($t(20)=-0.19$, $p=0.84$). The modulation of force with target width was nevertheless significant both in the CHOI and in the RND schedules ($\Delta F > 0$: CHOI: $t(20)=5.3$, $p<0.001$; RND: $t(20)=4.2$, $p<0.001$). Overall, these results suggest that despite being able to select the target width on each trial, there was only a limited modulation of the response to the perturbation with target width during the CHOI schedule compared to the BLK schedule.

In the CHOI schedule, participants were explicitly instructed to select the target width randomly before each trial. However, they were not able to do so. Most of the participants tended to select the narrow target for several trials in a row while they more often selected the wide target for a single trial before switching back to the narrow target. Therefore, after 80 trials, most participants had performed more trials with the

345 narrow target (on average, ~42 trials) than with the wide target (on average ~38 trials). The proportion of

346 single trials with the narrow and wide targets differed (narrow vs wide: 18% vs 25%, t(20)=-4.25,

347 p=0.0003). There were less isolated trials (hence, more trials in a row) for the narrow target than for the

348 wide target. If the participants wanted to minimize effort, they should have a bias towards the wide target

349 (i.e. they should have chosen the wide target more often than the narrow target).

350

Relationship between switching cost for motor and cognitive tasks.

352 The subjects who participated in the first experiment also participated in a cognitive switching task. In this

353 task, participants had to indicate either the shape or the color of a symbol that appeared in the middle of

354 the robot workspace (Fig. 1A). Subjects were able to learn the rules in a satisfactory way (RND: 85%

355 accuracy; BLK: 90% accuracy). When the task instruction changed randomly from trial to trial, the

356 reaction time of the participants was slightly above 1s (1085±47ms, mean ± SE). In contrast, the reaction

357 time when the task instruction remained unchanged for several trials in a row was 400ms shorter

358 (640±45ms, mean ± SE, t(20)=13.66, p<0.0001). These 400ms represent the switching cost between the

359 RND and BLK schedules (Fig.3A). Similarly, the switching cost in the motor task was around 0.3N,

360 which represents the difference in modulation of the force with target width between the RND and BLK

361 schedules (Fig. 3C). We found that the cognitive and motor switching costs were correlated across

362 participants (Fig.3B, r=0.57, t(20)=3.06, p=0.007). That is, participants for whom the schedule had a

363 small effect in the cognitive task (reaction time in RND not much worse than in BLK) were better able to

364 modulate their force in the RND schedule in comparison to the BLK schedule. This relationship suggests

365 that both motor and cognitive switching cost might stem from a general mechanism of the central nervous
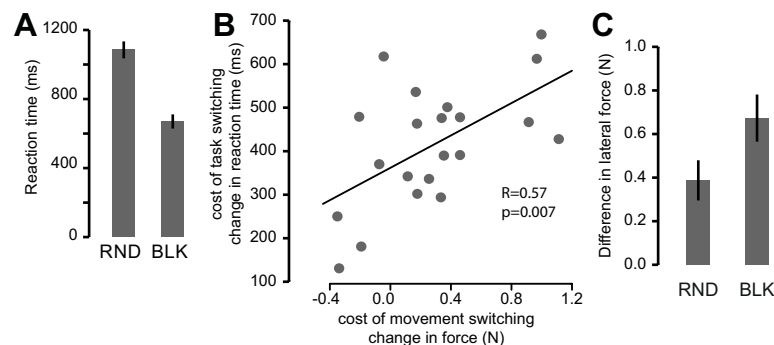
366 system.

Figure 3: Link between cognitive and motor switching cost. A) Reaction time (ms) in the random
(RND) and blocked (BLK) schedules during the cognitive task switching. The difference between the
two bars (RND-BLK) represents the average cognitive switching cost (ms). B) Correlation between the
cognitive and motor switching costs. C) Amount of modulation in the force exerted against the

372   perturbation with target width (force for narrow target minus force for wide target) for the RND and
373   BLK schedules. The difference between the two bars (BLK-RND) represents the motor switching cost
374   (N).

Knowledge of a better motor program is not used during a subsequent random schedule

375

376   The results from these experiments and previous studies on optimality of motor behaviors (de Rugy et al.,

377   2012; Kistemaker et al., 2014) are actually confounded by the possibility that participants might not know

378   what the optimal behavior is because they have never used it. Therefore, in the second experiment, we

379   tested whether the worst motor behavior observed during the random schedule was due to the inability to

380   use a better motor behavior or to the ignorance of a better one. Indeed, so far in all the experiments,

381   participants had always experienced the RND schedule before the BLK schedule. Again, we found in the

382   first random schedule that participants applied more force against a perturbation when the target was

383   narrow than when it was wide (paired t-test, $t(19)=2.37$, $p=0.028$). However, this difference between the

384   force applied against the perturbation for the narrow and wide targets was much larger during the blocked

385   schedule (interaction between schedule (RND1 and BLK) and target width, $F(1,19)=7.08$, $p=0.015$). We

386   then tested whether the participants were able to use the learned and better behavior in a second random

387   schedule (RND2). We found that, when participants experienced the random schedule again, the

388   difference in force applied against the narrow and wide targets was again smaller than the modulation of

389   force with target width observed during the blocked schedule (interaction between schedule – BLK and

390   RND2 - and target width, $F(1,19)=7.09$, $p=0.015$) and they did not differ significantly from the force in

391   the first random schedule (interaction between schedule – RND1 vs. RND2 - and target width:

392    $F(1,19)=0.25$, $p=0.62$). These data suggest that even though participants have used a better motor behavior

393   in the preceding blocked schedule, they were unable to use it during the following random schedule. In

394   other words, learning and using a better control policy in the blocked schedule does not lead to a better

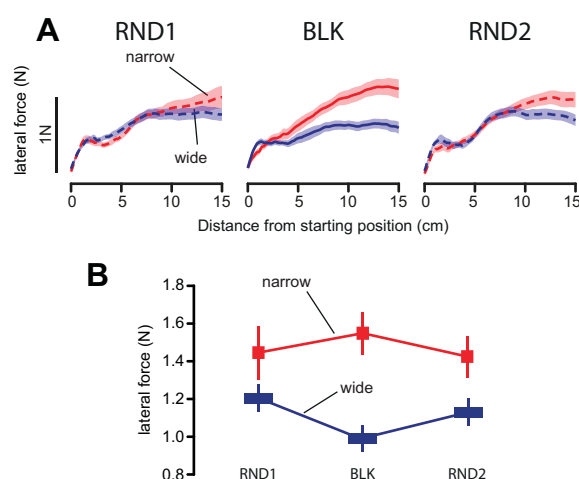395   performance in the subsequent random schedule.

396

Figure 4: Knowledge of a better motor program does not improve behavior in a subsequent random schedule A) Average force profiles across all participants recorded during the perturbation trials for each schedule (RND1 and RND2: random schedule; BLK: blocked schedule) and each target width separately (red: narrow target; blue: wide target). In these plots, the forces are represented against the distance from the starting position in order to match the level of perturbation. Shaded area around each curve represents standard error of the mean. B) Average force (N) recorded at 13 cm in the force profiles as a function of target width and schedule. Error bars are standard error of the mean.

Inability to instantaneously switch between motor programs

While the previous experiment aimed at emphasizing the inability to use a better motor program in the random schedule while knowing one, we wanted next to identify the cost of switching when target width changed unexpectedly during a blocked schedule. To do so, twenty other participants experienced a new schedule (MIX schedule) where 75% of the trials had a given target width (MIX-high: high probability trials, e.g. narrow target) and 25% (MIX-low: low probability trials) had the other target width (e.g. wide target). Half of these low probability trials were perturbation trials.
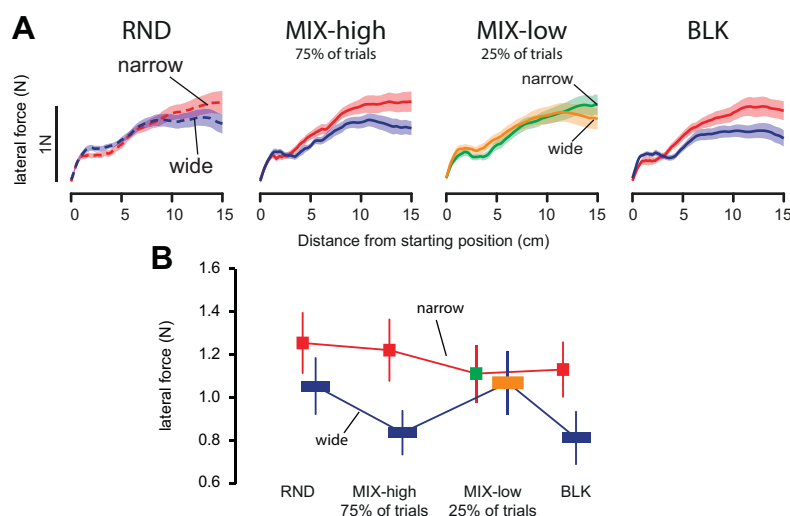

Figure 5: Change in motor program over one trial A) Average force profiles across all participants recorded during the perturbation trials for each schedule (RND: random schedule; MIX-high: high probability trials in the mixed schedule; MIX-low: low probability trials in the mixed schedule; BLK: blocked schedule) and each target width separately (red: narrow target; blue: wide target). In these plots, the forces are represented against the distance from the starting position in order to match the level of perturbation. Shaded area around each curve represents standard error of the mean. B) Average force (N) recorded at 13 cm in the force profiles as a function of target width and schedule. Error bars are standard error of the mean.

In this group, difference in force profiles were again more marked during the blocked schedule than during the random schedule. During the MIX schedule, the force that the participants exerted against the perturbation was clearly modulated by target width for the most frequent target width but not for the target width presented in the low-probability trials. These observations were confirmed by an interaction between target width and trial type (random, MIX-high, MIX-low and BLK: $F(3,57)=2.9267$, $p=0.041$). Post-hoc Tukey t-tests revealed that target width modulated force only for the high probability trials in the MIX schedule and for the blocked schedule ($p=0.001$ and $p=0.013$) but neither in the random schedule nor in the low probability trials ($p=0.31$ and $p=0.99$). A sizeable switch of control policy induced by a change in target width during the MIX blocks should result in a significant difference in force between low- and high-probability trials. While there was a trend towards significance when comparing trials with different target widths in the mix block with high probability of wide target (Tukey post-hoc: wide vs. narrow: $p=0.051$), there was no significant modulation of force with target width in the mix block with high probability of narrow targets (Tukey post-hoc: narrow vs. wide: $p=0.66$). In other words, the behavior in the low probability trials was close to what was observed in the random schedule.

Additional knowledge from our large pool of subjects (N=111).

In the three experiments presented here and the four ones presented in a previous paper (N=111 subjects), we found a very strong effect of schedules on the ability to modulate the response to a perturbation (Fig.6.A; interaction between target size and schedule (RND and BLK): $F(1,110)=35.18$, $p<0.00001$, partial eta square: 0.24). In order to take into account the different levels of force observed in the different experiments (e.g. due to reaching or shooting), this analysis was carried on the normalized lateral force (obtained by dividing the lateral force by the average force).

This database allows us to have a look on the actual difference between RND and BLK. Indeed, there appears to be quite some variability across experiments (Fig.6.B). While in some experiments (e.g. #1), the increase in force for the narrow target from RND to BLK was pronounced, it was absent or small in other experiments (#6 and #7). Similarly, for the wide targets, there was an important decrease in force from the RND to the BLK schedule is some experiments (e.g experiment #7) but not in others (e.g. #1). On average, on the basis of the 111 subjects, we can conclude that the schedule modulated the force both for the narrow target (RND vs. BLK: Tukey Post-Hoc: $p=0.0002$) and for the wide target (Tukey post-hoc: $p=0.0001$). This observation allows us to reject the possibility that subjects were lazy and pushing too hard for the wide target as a safety measure. In addition, we observe that the same control policy was not used

for both narrow and wide target in the RND condition given that the response to the perturbation was modulated by target width (Tukey Post-Hoc: narrow vs wide target in RND condition: p=0.0001). However, this modulation was smaller in the RND condition than in the BLK condition as indicated by the significant interaction.
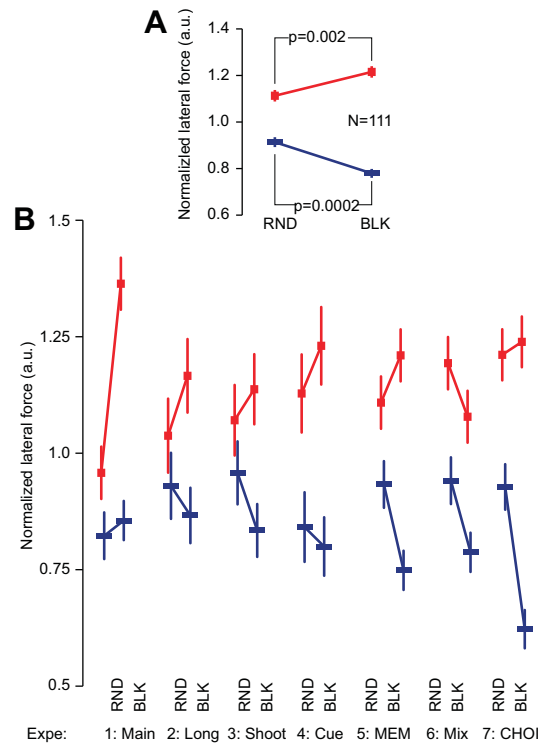

Fig.6: Analysis of the switching cost for the experiments reported in this paper (1 to 3) and in our previous (4: Main; 5: Long; 6: Shoot; 7: Cue experiments). Panel A: Normalized lateral force for the two schedules and target widths for the 111 subjects. B: Representation of the variability of the observed effect across the seven experiments. Error bars represent standard error of the mean.

Given the nature of the perturbation (position-dependent perturbation), it is difficult to judge how early the motor system responded differently to a narrow or wide target. Nonetheless, an ANOVA on force measures at a distance of 7cm (around 240ms after movement onset) from the starting point revealed the same target width x schedule interaction ($F(1,110)=37.8$, $p<00001$).

Absence of history effect in response to the perturbation

Costs in cognitive task switching are highlighted both by the difference between random and blocked schedules but also by a difference in performance between switch trials (previous trial had a different goal from the current one) and non-switch trials (previous trial was similar to the previous one).
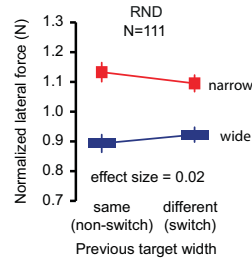
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Figure 7: History effect: influence of the target size from the previous trial on the normalized lateral force (N) exerted on the current trial. This graph summarizes the data from 111 participants (61 from this paper and 40 from Orban de Xivry 2013). Data from the RND schedules only. Error bars represent standard error of the mean.

In contrast to cognitive switching cost, we did not find differences in performance between switch (change in target width between the previous trial and the current one) and non-switch trials (same target width on the previous trial as on the current one). That is, we expected that the force to a perturbation would be larger on one trial when it was preceded by a trial with the narrow target and smaller when it was preceded by a trial with the wide target. In other words, we expected an interaction between target width and switching state (switch vs non-switch trials). In our large pool of participants (N=111, Fig.7), we found that the response to the perturbation was very weakly influenced by the switching (partial eta square: 0.02; $F(1,109)=2.06$, $p=0.15$). As always, the absence of significance could be due to an absence of power. For this reason, we reported the effect size of the effect: 0.02, which suggests that, even if the effect exist, it should be considered as a small effect (Cohen, 1988). In addition, such history-dependent effects, in other contexts, are typically observable with much smaller sample size (2 in Kowler et al., 1984; 8 in Witney et al., 2001; 10 in Franklin et al., 2008; 7 in Tabata et al., 2008). This suggests that the smaller modulation of the response to perturbation with target width during the random schedule is not due to the inability for the participants to converge to a better solution and that it is not a gradual process where participants adjusted their movement planning trial after trial.

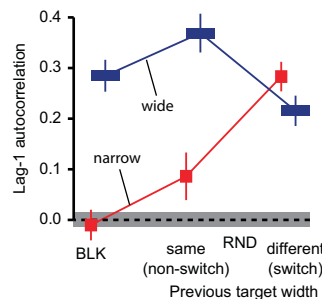**Trial-to-trial changes in the motor program**

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Figure 8: Trial-to-trial changes in movement endpoint: Lag-1 autocorrelation of movement endpoint error for different pairs of trials from the RND and BLK schedules. Error bars are standard error of the mean. The grey area represents a bootstrap estimate of the standard error of the autocorrelation when

496   pairs of trials are randomized. This graph summarizes the data from 111 participants (61 from this
497   paper and 40 from Orban de Xivry 2013).

498   Updating the planned direction of the next movement as a function of the error experienced in the

499   previous trial leads to low lag-1 autocorrelation between consecutive movement endpoint errors (van

500   Beers et al., 2013a). In contrast, a high lag-1 autocorrelation is associated with little or no trial-to-trial

501   changes in motor performance (similar to a random walk). In the three experiments presented here and the

502   four presented in a previous paper (N=111 participants), we found that, during the BLK schedule, the lag-

503   1 autocorrelation was almost zero for the narrow target but was much larger for the wide target (Fig.8;

504   N=111, -0,034±0.027 vs. 0.24±0.029, t(110)=-8.12, p<0.0001, partial eta square = 0.37). We also looked

505   at the lag-1 autocorrelation of endpoint error between pairs of trials with or without a change in target

506   width. During the random schedule, pairs of consecutive trials with narrow targets or with wide targets

507   exhibited the same behavior as in the BLK schedule (smaller for consecutive trials with the narrow target

508   than for consecutive trials with the wide target, 0.11±0.04 vs. 0.36±0.033, t(110)=-5.8, p<0.0001, partial

509   eta square = 0.24). This suggests that the small lag-1 autocorrelation was not due to a completely random

510   behavior (pure noise would also result in a zero auto-correlation) but to error correction. In contrast, a

511   change in target width appeared to reduce the ability to take the performance from the previous trial into

512   account as lag-1 autocorrelation between pairs of trials where the target width changed was high in both

513   cases (narrow to wide: 0.2±0.025; wide to narrow: 0.29±0.025). Overall we found an interaction between

514   switch and target width variables (Fig. 8, F(1,110)=47.6, p<0.0001). Post-Hoc test suggests that the lag-1

515   autocorrelation was lower for the pair of trials with narrow targets than for the three other pairs (Dunnett's

516   t-test: SS vs SL: p<0.001; SS vs LS: p= 0.023; SS vs LL: p<0.001). This pattern appears similar for the

517   two datasets (2013 vs. 2015; interaction between switch, target width and dataset: F(1,109)=.04468,

518   p=0.83).

519   In the BLK schedule, repetitiveness did not disengage the participants as they were more accurate and

520   more often inside the target in the blocked condition (46% of the time) than in the random condition for

521   the small target (40% of the time). Therefore, the success rate increased by 15% for the small target

522   between the RND and BLK conditions (t(110)=4.51, p=0.00002). So, even though the RND schedule was

523   potentially more engaging than the BLK schedule, participants were less successful during that schedule.

524   Finally, we did not notice any cost of switching in the median reaction time as confirmed by an ANOVA

525   on the median reaction time with schedule and target width as within-subject factors (main effect of target

526   width: F(1,110)=1.44, p=0.23, partial eta square = 0.012; interaction: F(1,110)=1.79, p=0.18).

Discussion

This study makes two important points about movement planning. First, the three experiments confirmed that the inability of our participants to behave optimally in a changing environment was consistent with the presence of a switching cost. More specifically, in our experiments, participants exhibited different motor behaviors in the random and blocked schedules, even when the participants themselves selected the width of the target that they will reach toward or when the participants have previously demonstrated the knowledge of a better motor program for the task at hand. They were also unable to switch from one control policy to another over one trial. Each of these experiments represents a critical test of the switching cost hypothesis for motor planning. Note that the switching cost should not be considered as a part of a general cost function to optimize the control policy. Rather, it should be linked to the limited flexibility in the random schedule compared to the blocked schedule. Second, participants were unable to use the endpoint error on one trial in order to adjust their planning of the next movement if the target width changed. These results directly speak over recent theories of motor planning (Wong et al., 2015), which suggest that movement initiation results from a series of processes that can be separated into two categories. Processes from the first category determine the motor goal (the 'what' pathway: target extraction and selection, attention, etc.) and are largely responsible for variation in reaction time while the processes of the second category are responsible for action selection and for the specification of the movement kinematics (the 'how' pathway). Given the absence of reaction time modulation in our task, we believe that our results speak directly to the limitations of the 'how' pathway, which encompasses both action selection and movement specification.

For the rest of the discussion, we will refer to the motor behaviors observed in the blocked scheduled as optimal. This claim of optimality can be viewed from two different perspectives. 1) Following optimal feedback control theory, the lateral force should be modulated with target width. Nobody can predict how much the lateral resistance should be modulated with target width in order to be considered optimal because the actual cost function is unknown but the blocked schedule is the best possible context to observe the optimal behavior. 2) Among all the behaviors observed in our study, behavior in the blocked schedule was the best one because it minimized error and energy. Such assertion is similarly used in several other studies (Liu and Todorov, 2007; Shadmehr et al., 2010; Nashed et al., 2012).

Reduced ability to learn from the error in the previous trial in order to adjust endpoint position

In simple reaching movements like in this study, action selection refers to the selection of the next aiming direction, which varies from trial-to-trial. Such trial-to-trial change in aiming direction has been

559   considered as a learning from error process where the aiming direction on a trial is equal to the aiming

560   direction on the previous trial plus a fraction of the error (van Beers, 2009; van Beers et al., 2013b). Such

561   a process causes the correlation of endpoint errors between two consecutive trials to be small if the errors

562   are taken into account (e.g. for the narrow target) and a positive auto-correlation when it is not (e.g. for a

563   wide target, where errors do not matter) (van Beers et al., 2013a). In the latter case, the planned movement

564   endpoint follows a random walk (van Beers et al., 2013a) where, in the absence of error correction,

565   movement endpoint on a given trial is more similar to movement endpoint on the previous trial than

566   chance. However, this theory is inconsistent with the auto-correlations observed during the random

567   schedule. When the target presented on one trial was narrow, participants updated the aiming direction for

568   their next trial only if the target on the next trial was also narrow but not if it was wide (Fig.8). This

569   suggests that the aiming direction cannot be updated before the target width of the next trial is known and

570   that participants held the error in memory until they saw the target width of the next trial. This scheme

571   appears very unlikely. If this scenario was possible, then the error observed in trials with wide target

572   should be used if the next target was narrow. To the contrary, the success rate in these trials with narrow

573   target was low compared to success rate in the BLK schedule. Alternatively, it is possible that the subjects

574   were unable to estimate the size of the error with respect to the center of the target because its ends were

575   too far away. We believe that this explanation does not hold as the wide target is 8cm wide (~9 deg of

576   visual angle) and people can accurately estimate the middle of a 20cm line in a line bisection task (error of

577   1% reported in Milner et al., 1992) or can accurately maintain their eye at the center of large targets (30

578   deg of visual angle) defined only by illusory contours (Wyatt et al., 1994).

579   The inability of our participants to adjust movement endpoint when target width changed suggests that an

580   alternative framework for the update of the aiming direction is necessary. This framework could have the

581   same characteristics as the Monte-Carlo Markov Chain framework (MCMC) proposed by Haith and

582   Krakauer (2014). In this framework, the update of the aiming direction does not depend on the error but

583   on the rewarding consequences of a trial (Skinner, 1981), which depends on target width as is the case for

584   optimal control (Nashed et al., 2012). This selection by consequences suggests that the reward received at

585   the end of the movement (i.e. the consequences) affects the future probability of selecting this motor

586   program in the future. The previous aiming direction is therefore replaced by the current one with some

587   probability that depends on the value of the previous and current aiming direction (Haith and Krakauer,

588   2014). However, the update of the aiming direction can only take place when the cost function is

589   unchanged between two consecutive trials as one cannot compare values from different scales (like

590   comparing apples and oranges). This would also explain why participants tended to repeat consecutive

591   trials with a narrow target (Fig. 2C) when asked to select the target width on each trial. Choosing the

592   narrow target repeatedly allowed them to update their aiming direction as a function of their past

593   performance. To summarize, the MCMC framework provides a convincing explanation for the absence of

594   updating of movement plans when target width changes and for the repetitive choice of the same target

595   width when the target is narrow.

Inability to be optimal

597   After action selection, the kinematics of the movement is specified through an independent process (Wong

598   et al., 2015). Our data suggest that the optimality of the control policy was disrupted by the frequent

599   changes in target width. Optimal control predicts that every movement should be optimal (Todorov and

600   Jordan, 2002; Nashed et al., 2012), independently of the schedule. However, we found that the modulation

601   of the response to perturbations with target width was much reduced but well present in the random

602   schedule compared to the blocked schedule. This contrasts with the absence of difference between the two

603   schedules observed in Nashed et al. (2012). However, their inability to detect the difference between the

604   two schedules might be due to the restricted number of participants per group (8 for RND and 8 for BLK)

605   and to their between-subject design. Accordingly, based on their quantitative data for the standard

606   deviation of reach endpoint, the effect seems more pronounced in the BLK (SD wide target: 2.5cm, SD

607   narrow target: 0.4cm) than in the RND schedule (SD wide target: 1.6cm, SD narrow target: 0.4cm).

608   This inability to modulate the feedback control policy adequately in the random schedule led to a cost in

609   accuracy and a cost in effort. Participants were unable to reach the same accuracy level for the narrow

610   target in the random schedule as in the blocked schedule and they spent too much energy controlling the

611   hand in the random schedule when the target was wide compared to in the blocked schedule. This

612   decrease in performance due to the randomization of condition is a general finding that extends far beyond

613   our simple task (Elliott and Allard, 1985; Edin et al., 1992; Horak and Diener, 1994; Khan et al., 2002;

614   Pruszynski et al., 2008; Afsanepurak et al., 2012). Here, we provide for the first time, an account for this

615   phenomenon.

616   This absence of optimality in the random schedule is not due to the long time required to reach the

617   optimality. Indeed, we observed an abrupt change in force response after the (unique) change in target

618   width in the blocked schedule (Orban de Xivry, 2013). Second, optimization of the control policy did not

619   lead to trial-to-trial changes in force response against the perturbation. Indeed, there was no effect of the

620   target width experienced on the previous trial on the force applied on the next trial (Fig.7). Therefore, this

621   suggests that our effect is not due to the fact that it takes several trials in order to reach the optimal

622   behavior. In contrast, in the blocked schedule, optimality was achieved in the first few trials (Orban de

623   Xivry, 2013). It also rejects the idea that performance in the random schedule is deteriorated due to a

624   history-dependent effect. In contrast, such history-dependent effects are observed in predictive eye

625 movements (Kowler et al., 1984; Tabata et al., 2008) for which the memory of target trajectory is updated

626 after each trial (Orban de Xivry et al., 2013) and for grasping movements where an internal model of the

627 object weight is built trial after trial (Johansson and Westling, 1988; Loh et al., 2010). Finally, our data

628 goes against the possibility that a single habitual control policy was used in the random schedule because

629 we observed a significant modulation of the behavior with target width in the random schedule as well.

630 The origin of this modulation in the random schedule remains unresolved. We can only speculate about

631 how the brain achieves this feat. It might be that an intermediate control policy is used given the

632 uncertainty about target width (Haith et al., 2015; Gallivan et al., 2016). Alternatively, it might be that the

633 observed response is the sum of two independent processes (Kurtzer et al., 2014), only one of which is

634 limited by the switching cost. Finally, it might be that two different control modes are used in these

635 contexts, one optimal and one robust (Crevecoeur et al., 2014). In this context, the absence of difference

636 between switch and non-switch trials (Fig.7) can be explained by the fact that there is full flexibility in the

637 RND schedule but within tighter limits allowed by the control policy.

638 This is obviously not the first study to demonstrate a lack of optimality in motor behaviors. However, the

639 previous studies required the learning of a new control policy in a new and unknown environment or with

640 a new tool (Hudson et al., 2010; Kistemaker et al., 2010, 2014; de Rugy et al., 2012; Zhang et al., 2012).

641 That is, the participants from these studies never exhibited the optimal motor behavior and it is unknown

642 whether participants would have been able to execute the optimal motor behavior. In contrast, in the

643 present study, we show that the participants knew the optimal control policy because they exhibited it in

644 the blocked schedule. However, a switching cost prevented them from using the same policy in the

645 random schedule. In other words, while previous studies demonstrated that we cannot always find the

646 optimal motor behavior, the present study demonstrates that even if you have found it (e.g. in the blocked

647 schedule), you might not be able to use it (e.g. in the random schedule). Indeed, in experiment 2, despite

648 having used a better (more accuracy for the narrow target and less energy wasted for the wide target)

649 feedback control policy in the blocked schedule, participants were unable to use these control policies in

650 the subsequent random schedule. This observation supports our claim that movements in the random

651 schedule were not optimal when compared to the blocked schedule and confirms the existence of a cost

652 associated with changing the feedback control policy, i.e. a switching cost. If no such cost existed, then

653 participants could use their best (less costly) strategy to perform the task (the one used in the blocked

654 schedule).

655 In the case of multiple targets, several motor programs are prepared together during the planning stage

656 (Cisek and Kalaska, 2005, 2010) and the non-selected one is later inhibited. The current study leads to the

657 question of whether there are multiple programs prepared when a unique target location must be

658 associated with two different control policies for the narrow and wide targets (Gallivan et al., 2016)? In

659 this case, inhibition of the non-selected motor program could lead to subsequent switching cost as it

660 became harder to retrieve the inhibited motor program (Duque et al., 2005; Duque and Ivry, 2009; Mars et

661 al., 2009) or the inhibited cognitive task (Mayr et al., 2000, 2006). Alternatively, the switching cost might

662 arise from the fact that a new control policy must be selected each time the target width changes.

663 We do not question the fact that, following optimal feedback control, feedback gains are determined

664 before movement in order to bring the hand on the target or to respond to potential perturbations during

665 the movement. However, we want here to highlight that this optimization of the feedback control law is

666 not as flexible as suggested by many authors and that switching between control policies carry some costs.

667 Finally, the inability of our participants to learn from the errors observed on the previous trials when target

668 width changed and to modulate the feedback gains appropriately in the random schedule reflect two

669 independent limitations of the planning of movements. Indeed, the aiming direction is updated by the

670 observed endpoint errors but there is no particular reason to update the control policy in function of this

671 error. In addition, a switch in target width had a major effect on the update of the aiming direction (Fig.8)

672 but had no effect on force modulation (Fig.7). Accordingly, an update of the control policy following the

673 MCMC framework would lead to a history effect for the force modulation, which was not observed

674 (Fig.7). As outlined by Wong and colleagues, action selection (choosing the aiming direction) and

675 movement specification (choosing the control policy) are two independent processes.

How similar is the phenomenon described here to cognitive task switching

677 The motor switching cost identified here based on force modulation with schedules bears many

678 similarities with the switching cost for cognitive tasks. However, it also differs from it in a number of

679 ways. First, while we identified here a switching cost for the 'how pathway' (Wong et al., 2015), cognitive

680 studies typically focus on a cost on the 'what pathway' which results in an effect on the reaction time

681 (Rogers and Monsell, 1995). It is unknown whether a switching cost for the "how" pathway exists in

682 cognitive tasks while we demonstrated it for motor tasks. The observation that the switching cost in our

683 task did not affect the reaction time is consistent with the fact that movement preparation and initiation are

684 two independent processes (Haith et al., 2016) and that several factors directly influence the feedback

685 control policy but do not modulate the reaction time. For instance, the influence of target size on reaction

686 time is very limited (Quinn et al., 1980). It is believed that the feedback control policy is only selected

687 among several possibilities. Such process does not largely influence the reaction time.

688 Despite this difference, self-selection of target (experiment 1) or selection of cognitive task rule

689 (Arrington and Logan, 2004) does not abolish the switching cost. Second, while a switching cost can be

690   identified on a single trial basis in cognitive tasks (reaction time is different in switch and non-switch

691   trials), we failed to identify such effect in our data (Fig.7). However, we found that the switch prevented

692   participants from taking the performance of the previous trial into account in order to update their

693   movement plan for the next trial (Fig.8).

694   Finally, we found that motor and cognitive switching costs were correlated across participants. This

695   correlation might stem from the fact that updating the association between a stimulus and a motor program

696   might be controlled by a mechanism that is independent of the rationale behind the update (i.e. change in

697   task rule or change in target width) such as the one taking place in the premotor and motor areas for

698   cognitive and motor tasks. Cells from the cingulate cortex are differentially modulated when the

699   movement plan needs to be updated or when it needs to be repeated (Shima and Tanji, 1998; Procyk et al.,

700   2000). Lesions of the same area impair performance at a cognitive switching task in monkeys (Rushworth

701   et al., 2003). The pre-supplementary and supplementary motor areas (Nachev et al., 2008) appear to also

702   play an important role in the cognitive and motor switching processes. Cells of the pre-supplementary and

703   supplementary motor areas only responded before switch trials and not before non-switch trials during a

704   reaching task to two targets (Matsuzaka and Tanji, 1996). Similarly, pre-SMA first inhibits the previous

705   motor program and then boosts the desired saccade when instructed to switch (Isoda and Hikosaka, 2007;

706   Hikosaka and Isoda, 2010).

707 **Conclusion**

708 A simple manipulation of target width during a reach experiment reveals the limitations of the

709 mechanisms of motor planning. These data reveal that action selection might proceed via a selection by

710 consequence mechanism and that movement specification suffers from a switching cost for motor

711 planning. This switching cost for motor tasks shares many similarities with the switching cost identified in

712 cognitive tasks.

713

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871

872

Figure Legends

Figure 1: Experimental protocols. A) Cognitive task switching: participants had to indicate the shape of the symbol (shape task: square or circle) if a white line was displayed above the symbol on the screen (as on the panel) or its color (color task: orange or green) if the line was below it (at the place of the dashed line). The response was indicated by exerting an isometric force on the left or right handle of the robot manipulandum. The situation depicted on the figure requires a left hand response. The hands were not visible for the participants. B) Motor task switching: In this task, participants were instructed to bring the cursor through the aperture of a circle. This aperture was always at the same location but could have one of two possible widths (0.8 or 8cm). Each trial started with the appearance of the starting position (Black square, return and cue phase). During this phase, a cue indicated the width of the aperture for the ensuing trial (grey symbol, Return and Cue phase). The target was then presented 15 cm away from the starting position in front of the participant (Target phase). When the participants initiated their reach, the hand cursor was replaced by a circle whose radius increased with the distance travelled by the hand (Movement phase). Veridical hand position was provided after movement end in order to provide feedback about movement accuracy (feedback phase). Additional information was provided via the imprint that the hand left on the circle when it crossed it. The imprint was blue if movement duration was too long, yellow if movement duration was too short and green if movement duration was between 500 and 600ms. One point could be earned for good movement speed and another point could be earned for good accuracy. The total number of points collected so far during the block was displayed at the end of each trial (156 points in the illustration). For clarity purpose, actual colors used in the experiments are not represented on the illustration but are used in the text. C) The three panels illustrate the repartition of trials with the narrow and wide target over the course of the three experiments (see main text). The y-axis represents target width and the x-axis trial number. In the CHOI schedule, participants selected the width of the target for each trial and were instructed to do so randomly. In the random schedule, target width was randomly varied from trial-to-trial. In the blocked schedule, target width remained unchanged for either 45 trials (experiment 1) or 60 trials (experiments 2 and 3). The order of target width was counterbalanced across participants. In the MIX schedule, there was an imbalance in the percentage of trials for each target width (75% - high probability trials vs 25% - low probability trials). Each participant received 60 trials with higher probability of one target width followed by another series of 6o trials where the other target width was more frequent. The order was also counterbalanced across participants.

Figure 2: Self-selection of target width does not improve optimality of behavior in comparison with the random schedule. A) Average force profiles across all participants recorded during the perturbation trials for each schedule (CHOI: self-selection of target width; RND: random schedule; BLK: blocked schedule) and each target width separately (red: narrow target; blue: wide target). In these plots, the forces are represented against the distance from the starting position in order to match the level of perturbation. Shaded area around each curve represents standard error of the mean. B) Average force (N) recorded at 13 cm in the force profiles as a function of target width and schedule. Error bars are standard error of the mean. C) Average distribution of the length of series of trials with the same target width (i.e. how many trials in a row had the same target width). Error bars are standard error of the mean. Inset in panel C) Proportion of trials where the target width is different from the target width on the previous and next trials.

Figure 3: Link between cognitive and motor switching cost. A) Reaction time (ms) in the random (RND) and blocked (BLK) schedules during the cognitive switching task. The difference between the two bars (RND-BLK) represents the average cognitive switching cost (ms). B) Correlation between the cognitive and motor switching costs. C) Amount of modulation in the force exerted against the perturbation with target width (force for narrow target minus force for wide target) for the RND and BLK schedules. The difference between the two bars (BLK-RND) represents the motor switching cost (N).

Figure 4: Knowing the optimal motor program does not improve behavior in a subsequent random schedule A) Average force profiles across all participants recorded during the perturbation trials for

each schedule (RND1 and RND2: random schedule; BLK: blocked schedule) and each target width separately (red: narrow target; blue: wide target). In these plots, the forces are represented against the distance from the starting position in order to match the level of perturbation. Shaded area around each curve represents standard error of the mean. B) Average force (N) recorded at 13 cm in the force profiles as a function of target width and schedule. Error bars are standard error of the mean.
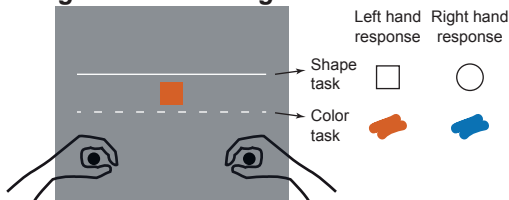
Figure 5: Change in motor program over one trial A) Average force profiles across all participants recorded during the perturbation trials for each schedule (RND: random schedule; MIX-high: majority of trials in the mixed schedule; MIX-low: low probability trials in the mixed schedule; BLK: blocked schedule) and each target width separately (red: narrow target; blue: wide target). In these plots, the forces are represented against the distance from the starting position in order to match the level of perturbation. Shaded area around each curve represents standard error of the mean. B) Average force (N) recorded at 13 cm in the force profiles as a function of target width and schedule. Error bars are standard error of the mean.

Fig.6: Analysis of the switching cost for the experiments reported in this paper (1 to 3) and in our previous (4: Main; 5: Long; 6: Shoot; 7: Cue experiments). Panel A: Normalized lateral force for the two schedules and target widths for the 111 subjects. B: Representation of the variability of the observed effect across the seven experiments. Error bars represent standard error of the mean.
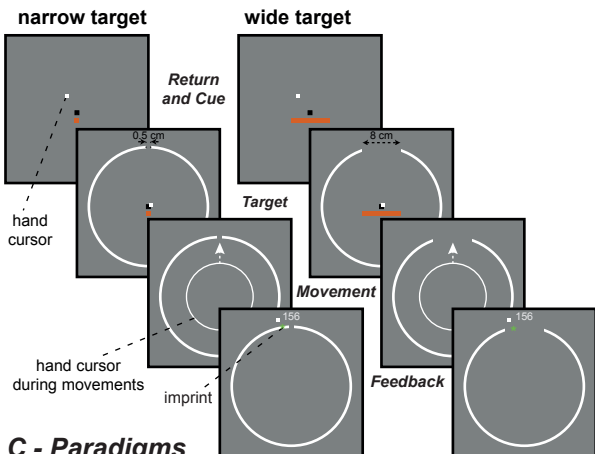
Figure 7: History effect: influence of the target size from the previous trial on the force (N) exerted on the current trial. This graph summarizes the data from 111 participants (61 from this paper and 40 from Orban de Xivry 2013). A) Data from the RND schedules only.

Figure 8: Trial-to-trial changes in movement endpoint: Lag 1 autocorrelation of movement endpoint error for different pairs of trials from the RND and BLK schedules. Error bars are standard error of the mean. This graph summarizes the data from 111 participants (61 from this paper and 40 from Orban de Xivry 2013).
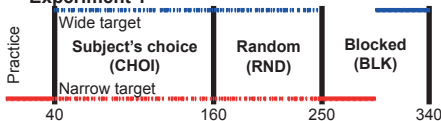
A - Cognitive switching task

Left hand response   Right hand response

Shape task

Color task

B - Motor switching task

narrow target   wide target

Return and Cue

0.5 cm   8 cm

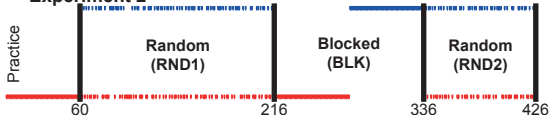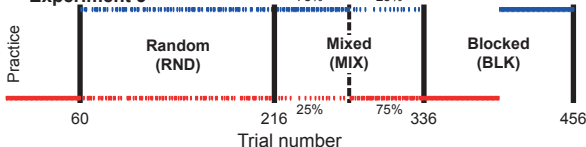hand cursor

Target

Movement

hand cursor during movements

imprint

156   156

Feedback

C - Paradigms

Experiment 1

Practice

Wide target

Subject's choice (CHOI)   **Random (RND)**   **Blocked (BLK)**

Narrow target

40   160   250   340

Experiment 2

Practice

Random (RND1)   **Blocked (BLK)**   **Random (RND2)**

60   216   336   426

Experiment 3

Practice

75%   25%

Random (RND)   **Mixed (MIX)**   **Blocked (BLK)**

25%   75%

60   216   336   456

Trial number

A CHOI RND BLK

lateral force (N)

narrow

wide

1N

Distance from starting position (cm)

0 5 10 15 0 5 10 15 0 5 10 15

B

lateral force (N)

narrow

wide

1.8
1.6
1.4
1.2
1.0
0.8
0.6

CHOI RND BLK

C

# of observations

Percentage of trials
that are singletons

12
10
8
6
4
2
0

28

wide

narrow

16

1 2 3 4 5

length of series with same target width choice

A
Reaction time (ms) — RND, BLK

B
cost of task switching change in reaction time (ms) vs cost of movement switching change in force (N)

R=0.57
p=0.007

C
Difference in lateral force (N) — RND, BLK

A

narrow

lateral force (N)

1N

wide

RND1   BLK   RND2

Distance from starting position (cm)

B

lateral force (N)

1.8
1.6
1.4
1.2
1.0
0.8

narrow

wide

RND1   BLK   RND2

A

RND MIX-high MIX-low BLK
75% of trials 25% of trials

narrow

wide

narrow

wide

lateral force (N)

1N

Distance from starting position (cm)

B

lateral force (N)

narrow

wide

RND MIX-high MIX-low BLK
75% of trials 25% of trials

A

Normalized lateral force (a.u.)

p=0.002

N=111

p=0.0002

RND   BLK

B

Normalized lateral force (a.u.)

Expe: 1: Main   2: Long   3: Shoot   4: Cue   5: MEM   6: Mix   7: CHOI