

Impact of a demanding movement on decision-making

1           **Humans sacrifice decision-making for action**  
2                   **execution when a demanding control of**  
3                           **movement is required**

6           Amélie J. REYNAUD, Clara SALERI LUNAZZI, David THURA

7                           *Lyon Neuroscience Research Center – Impact team*  
8                           *Inserm U1028 – CNRS UMR5225 – Lyon University*

11                           *Running head*

12                           Impact of a demanding movement on decision-making

14                           *Corresponding author information*

15                           David Thura

16                           Lyon Neuroscience Research Center – Impact team  
17                           Inserm U1028 – CNRS UMR5225 – Lyon University  
18                           16 avenue du Doyen Lépine, 69675 Bron, France  
19                           Phone : +33 4 72 91 34 14  
20                           E-mail: david.thura@inserm.fr

23                           *Manuscript information*

24                           Total word count: ~10700; 40 pages; 8 figures

26                           *Conflict of interest*

27                           The authors declare no competing financial interests

29                           *Funding*

30                           This work was supported by a CNRS/Inserm ATIP/Avenir grant and an Inserm young  
31                           investigator fellowship to DT

## Impact of a demanding movement on decision-making

32

### ABSTRACT

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

52

### NEW & NOTEWORTHY

53

54

55

A growing body of evidence suggests that decision-making and action execution are governed by partly overlapping operating principles. Especially, previous work proposed that a shared decision urgency/movement vigor signal, possibly computed in the basal ganglia, coordinates both deliberation and movement durations in a way that maximizes the reward rate. Recent data support one aspect of this hypothesis, indicating that the urgency level at which a decision is made influences the vigor of the movement produced to express this choice. Here we investigated whether conversely, the motor context in which a movement is executed determines decision speed and accuracy. Twenty human subjects performed a probabilistic decision task in which perceptual choices were expressed by reaching movements toward targets whose size and distance from a starting position varied in distinct blocks of trials. We found strong evidence for an influence of the motor context on most of the subjects' decision policy but contrary to the predictions of the "shared regulation" hypothesis, we observed that slow movements executed in the most demanding motor blocks in terms of accuracy were often preceded by faster and less accurate decisions compared to blocks of trials in which big targets allowed expression of choices with fast and inaccurate movements. These results suggest that decision-making and motor control are not regulated by one unique "invigoration" signal determining both decision urgency and action vigor, but more likely by independent, yet interacting, decision urgency and movement vigor signals.

Recent hypotheses propose that choices and movements share optimization principles derived from economy, possibly implemented by one unique context-dependent regulation signal determining both processes speed. In the present behavioral study conducted on human subjects,

## Impact of a demanding movement on decision-making

56 we demonstrate that action properties indeed influence perceptual decision-making, but that  
57 decision duration and action vigor are actually independently set depending on the difficulty of  
58 the movement executed to report a choice.

59

60

## KEYWORDS

61

Decision-making, Reaching, Urgency, Speed-accuracy trade-off, Human

## Impact of a demanding movement on decision-making

62  
63  
64  
65  
66  
67  
68  
69  
70  
71  
72  
73  
74  
75  
76  
77  
78  
79  
80  
81  
82  
83  
84

INTRODUCTION

Animals, including humans, are faced with decisions about actions on a daily basis, and they behave to seek rewards while avoiding punishments and minimizing energy expenditure. Because the evaluation of reward, risk, and effort governs our action choices, investigating how the brain processes these variables is critical to improve our understanding of adapted or dysfunctional goal-directed behavior.

Importantly, the subjective value of a given activity is not only limited to its related reward, risks, and efforts. It also depends on the amount of time invested in it, as time strongly discounts the value of rewards (Myerson and Green, 1995). Therefore, what is ultimately most adaptive is to choose options that maximize one's global reward rate (Bogacz et al., 2010; Balci et al., 2011), which occurs when the decision and action processes are sufficiently accurate but not overly effortful and time-consuming. As a consequence, nearly all decision scenarios present decision-makers with speed-accuracy-effort trade-offs during both decision-making and action execution, and the brain must control both processes to maximize the rate of reward.

Because trade-offs during decision and action have been typically studied in isolation, mechanisms allowing a coordinated maximization of reward rate are still elusive. Recent promising advances suggest, however, that motor control and choices, including economic ones, are governed by partly overlapping optimization principles (Shadmehr et al., 2010, 2019; Haith et al., 2012; Choi et al., 2014; Yoon et al., 2018; Carland et al., 2019). First, human and non-human primates move faster and with a shorter reaction time toward items that they value more (Kawagoe et al., 1998; Summerside et al., 2018; Revol et al., 2019). Second, humans take motor costs into account during both motor (Cos et al., 2011, 2012, 2014; Morel et al., 2017) and non-motor (Burk et al., 2014; Marcos et al., 2015; Diamond et al., 2017; Hagura et al., 2017)

## Impact of a demanding movement on decision-making

85 decisions and effortful reaches impose a cost for decision-making similar to cost functions in  
86 motor control (Wickler et al., 2000; Shadmehr et al., 2016; Morel et al., 2017; Reppert et al.,  
87 2018). Finally, in the foraging paradigm where one makes decisions regarding how long to stay  
88 and accumulate reward from one patch, and then moves with certain speed to another patch, the  
89 goods collection duration and the vigor (movement speed and duration) with which human  
90 subjects move from one reward site to another are governed by a mechanism allowing to  
91 maximize the overall capture rate (Yoon et al., 2018).

92 In line with this shared optimization hypothesis, we and others have proposed that control of  
93 urgency is critical for reward rate maximization during decision-making between actions  
94 (Ditterich, 2006; Churchland et al., 2008; Standage et al., 2011; Thura et al., 2012; Malhotra et  
95 al., 2017, 2018). Urgency is a context-dependent, motor-related signal that grows over the time  
96 course of deliberation, pushing the decision-related neural activity toward the commitment  
97 threshold (Thura and Cisek, 2014; Kira et al., 2015; Murphy et al., 2016; Steinemann et al.,  
98 2018). Remarkably, we demonstrated in a changing evidence decision task that urgency level at  
99 decision time strongly influences speed and duration of the following motor commands: early  
100 decisions, usually made based on strong sensory evidence but low urgency, were followed by  
101 long movements (in terms of duration) whereas late decisions, relying on weak sensory evidence  
102 but strong urgency, were followed by faster movements. Then, when subjects were encouraged to  
103 make faster and less accurate decisions in distinct blocks of trials, movements were faster  
104 compared to blocks encouraging slow and accurate choices. These results imply that a shared  
105 invigoration signal, possibly computed in the basal ganglia, coordinates the unified adaptation of  
106 the speed-accuracy trade-off during both decision-making and action execution in order to

## Impact of a demanding movement on decision-making

107 control the rate of reward (Thura et al., 2014; Thura and Cisek, 2016, 2017; Cisek and Thura,  
108 2018; Thura, 2020).

109 We proposed a model of this hypothetical mechanism, labeled the “shared regulation” hypothesis  
110 (Figure 1A, Thura et al., 2014). In this model, speed-accuracy trade-offs for deciding and acting  
111 are influenced by a shared decision urgency/movement vigor signal. As a consequence, the  
112 context-dependent urgency level at which a decision is made should determine the vigor  
113 (duration and speed scaled by amplitude) of movements produced to express this choice and  
114 conversely, the context-dependent vigor of movements executed to express a choice should  
115 predict the level of urgency with which that choice is made. Recent behavioral and  
116 neurophysiological data collected in both trained monkeys and naïve humans strongly support the  
117 former prediction (Thura et al., 2014; Thura and Cisek, 2016; Thura, 2020). The latter prediction,  
118 namely whether or not the fastest choices are made in motor contexts encouraging the most  
119 vigorous movements (Figure 1B), remains, however, to be tested.

120 To this aim, we conducted an experiment in which human subjects performed a probabilistic  
121 decision task in which perceptual choices were expressed by reaching movements toward targets  
122 whose size and distance from the starting point varied across blocks of trials, allowing us to  
123 assess the effects of the motor context on subjects’ decision policy. In the present work, the speed  
124 and duration of the movements are considered as indicators of action vigor and the movement  
125 speed-accuracy trade-off are used to modulate this vigor.

126

## 127 MATERIALS AND METHODS

128 *Participants*

## Impact of a demanding movement on decision-making

129 Twenty-three healthy, human subjects (ages: 18-41; 17 females; 21 right-handed) participated in  
130 this study. All gave their consent orally before starting the experiment. The ethics committee of  
131 Inserm (IRB00003888) approved the protocol on March 19<sup>th</sup>, 2019. Each participant was asked to  
132 perform two experimental sessions. They received monetary compensation (20 € per completed  
133 session) for participating in this study. Among them, twenty (ages: 20-41; 16 females; 18 right-  
134 handed) completed at least two sessions and have thus been included in the present dataset.

### 135 *Dataset*

136 The decision and motor behaviors of most of the subjects (17/20) have been described in a recent  
137 publication aimed to report the effect of decision strategy on movement properties in human  
138 subjects (Thura, 2020). This analysis showed that according to the shared regulation hypothesis,  
139 the urgency level at the time of decision commitment strongly influences movement kinematics,  
140 with urgency-based decisions leading to vigorous movements. In the present paper, we analyzed  
141 data of the same subjects along with data from 3 additional ones, but we grouped trials depending  
142 on movement constraints (target size/movement amplitude configurations, see below), allowing  
143 us to test on the same subjects the reverse side of the shared regulation hypothesis, i.e. the effects  
144 of motor context on decision policy.

### 145 *Setup*

146 The subjects sat in an armchair made planar reaching movements using a handle held in their  
147 dominant hand (Figure 2A). A digitizing tablet (GTCO CalComp) continuously recorded the  
148 handle horizontal and vertical positions (100 Hz with 0.013cm accuracy). Target stimuli and  
149 cursor feedback were projected by a DELL P2219H LCD monitor (60 Hz refresh rate) onto a  
150 half-silvered mirror suspended 26 cm above and parallel to the digitizer plane, creating the  
151 illusion that targets floated on the plane of the tablet. Unconstrained eye movements and pupil

## Impact of a demanding movement on decision-making

152 area of a subset of subjects were recorded using an infrared camera (ISCAN, sampling rate of 120  
153 Hz, data not shown).

### 154 *Tasks*

155 The subjects performed a modified version of the tokens task (Figure 2B, see Cisek et al., 2009  
156 for the original version). They were faced with a visual display consisting of three blue circles  
157 (1.5 cm radius) placed horizontally at a distance of 6 cm of each other (the “decision” stimuli). In  
158 the central blue circle, 15 small tokens were randomly arranged. Positioned 12 cm below, three  
159 black circles, organized horizontally as well defined the “movement” stimuli. While the central  
160 black circle radius was kept constant at 0.75 cm, the size of the two lateral black circles and their  
161 distance from the central circle could vary, set to either 0.75 (small) or 1.5 cm (big) of radius, and  
162 either 6 (short) or 12 cm (long) of distance from the central circle, in distinct blocks of trials. This  
163 design allowed us to define four motor blocks depending on the size/distance combination of the  
164 two targets: “small/short”, “small/long”, “big/short” and “big/long” (Figure 2C).

165 A trial was initiated when the subject moved and hold the handle into the small black central  
166 circle (starting position) for 500ms. Tokens then started to jump, one by one, every 200ms in one  
167 of the two possible lateral blue circles. The subjects’ task was to decide which of the two lateral  
168 blue circles would receive the majority of the tokens at the end of the trial. They reported their  
169 decisions by moving the handle into the lateral black circle corresponding to the side of the  
170 chosen blue circle. Importantly, subjects were allowed to make and report their choice at any time  
171 between the first and the last jump. Arm movement duration could not exceed 800ms,  
172 irrespective of the motor block. If a movement exceeds 800ms (too slow) or if it reaches the  
173 target but fails to stop in it within 800ms (inaccurate), the trial is considered as a movement error  
174 trial. Once the choice is properly reported, the remaining tokens jumped more quickly to their



## Impact of a demanding movement on decision-making

175 final circles. In separate blocks of trials, this post-decision interval was set to either 20ms (“fast”  
176 decision block) or 150ms (“slow” decision block). The acceleration of the remaining tokens  
177 implicitly encouraged subjects to decide before all tokens had jumped into their respective lateral  
178 circles, to save time and increase their rate of reward. Note that each reaching movement carries a  
179 temporal cost with respect to reward rate maximization (see equation 3) because the remaining  
180 tokens accelerate only when action is completed. After holding the handle in the target for  
181 500ms, visual feedback about decision success or failure (the chosen decision circle turning  
182 either green or red, respectively) was provided after the last token jump. A 1500ms period (the  
183 inter-trial interval) preceded the following trial.

184 Before and after the tokens task described above, each subject also performed 100 trials of a  
185 delayed reach task (DR task). This task was identical to the tokens task except that there was only  
186 one lateral decision circle displayed at the beginning of the trial (either at the right or the left side  
187 of the central circle with 50% probability) and all tokens moved from the central circle to this  
188 unique circle at a GO signal occurring after a variable delay ( $1000 \pm 150$ ms). They executed 2  
189 different motor blocks of 25 trials each before the tokens task and the 2 other motor blocks (25  
190 trials each) after the tokens task. This DR task was used to estimate the sum of the delays  
191 attributable to sensory processing of the stimulus display as well as to response initiation in each  
192 motor condition.

### 193 *Instructions*

194 In a given session, subjects were asked to complete one slow decision block and one fast decision  
195 block of the tokens task. To complete a decision block (either fast or slow), subjects had to make  
196 160 correct choices, indirectly motivating them to optimize successes per unit of time. After the  
197 first block was completed, a short break was offered to the subject. Within each decision block,

## Impact of a demanding movement on decision-making

198 the size of the movement targets and their distance from the starting circle, i.e. the motor blocks,  
199 were varied every 40 trials. In a session, each motor block was thus performed twice, once in the  
200 slow decision block, and once in the fast decision block.

201 Subjects performed two sessions (test-retest design), one a day, and each of them separated by a  
202 maximum of 7 days. In session #1 subjects always started the tokens task in the slow decision  
203 block with the following succession of motor blocks: small/short, small/long, big/short, and  
204 big/long; followed by the execution of the fast decision block with the same motor blocks order.  
205 To prevent any block-related confounding effect, the order of decision and motor blocks  
206 presentation was reversed in session #2. Before the first session, we explicitly described to the  
207 subjects the principle of each decision block, specifying that deciding quickly in the fast block  
208 was more advantageous in terms of time-saving than in the slow block (because of the larger  
209 acceleration of the remaining tokens) but that such hasty behavior could also lead to more  
210 erroneous decisions. A short recall was provided before starting the second session. Because  
211 subjects were informed that they had to complete a given number of correct responses in each  
212 session, they were all aware that they were presented with a speed/accuracy trade-off in this task.  
213 A practice period consisting of performing 20 tokens task trials in the slow decision and big/short  
214 motor blocks was proposed at the beginning of the first session, mainly allowing subjects to get  
215 familiar and comfortable with the manipulation of the handle on the tablet. Among the 23  
216 subjects who participated in this study, two have been tested six and seven times. The additional  
217 sessions performed by these two subjects are not described in the present report.

## 218 *Data analysis*

219 All arm movement data were analyzed off-line using MATLAB (MathWorks). Reaching  
220 characteristics were assessed using the subjects' movement kinematics. Horizontal and vertical

## Impact of a demanding movement on decision-making

221 position data were first filtered using a tenth-degree polynomial filter and then differentiated to  
222 obtain a velocity profile. Onset and offset of movements were determined using a 3.75 cm/s  
223 velocity threshold. Peak velocity was determined as the maximum value between these two  
224 events and endpoint error was defined as the Euclidian distance separating the target center from  
225 the movement endpoint location. The dispersion of movement end-points is visualized with  
226 confidence ellipses representing an iso-contour of the Gaussian distribution, defining the region  
227 that contains 95% of all samples in each condition.

228 We computed at each moment during a trial the success probability  $p_i(t)$  associated with choosing  
229 each target  $i$ . For a total of 15 tokens, if at a particular moment in time the right target contains  $N_R$   
230 tokens, whereas the left contains  $N_L$  tokens, and there are  $N_C$  tokens remaining in the center, then  
231 the probability that the target on the right will ultimately be the correct one (i.e., the success  
232 probability of guessing right) is as follows:

$$p(R|N_R, N_L, N_C) = \frac{N_C!}{2^{N_C}} \sum_{k=0}^{\min(N_C, 7-N_L)} \frac{1}{k!(N_C - k)!} \quad (1)$$

233 To characterize the success probability profile of each trial, we calculated this quantity (with  
234 respect to either the correct target or the target ultimately chosen by the subject, depending on  
235 purposes) for each token jump. To ensure that the difficulty of decisions was homogeneous  
236 among subjects and experimental conditions, we controlled the sequence of trials experienced by  
237 subjects in each session. Especially, we interspersed among fully random trials (20% of the trials  
238 in which each token is 50% likely to jump into the right or the left lateral circle) three special  
239 types of trials characterized by particular temporal profiles of success probability. Subjects were  
240 not told about the existence of these trials. 30 % of trials were so-called “easy” trials, in which  
241 tokens tended to move consistently toward one of the circles, quickly driving the success

## Impact of a demanding movement on decision-making

242 probability  $p_i(t)$  for each toward either 0 or 1. Another 30% of trials were “ambiguous”, in which  
243 the initial token movements were balanced, making the  $p_i(t)$  function close to 0.5 until later in the  
244 trial. The last special trial type was called “misleading” trials (20%) in which the 2-3 first tokens  
245 jumped into the incorrect circle and the remaining ones into the correct circle. In all cases, even  
246 when the temporal profile of success probability of a trial was predesigned, the actual correct  
247 target was randomly selected on each trial. Importantly, the sequence of trials was designed such  
248 as the proportion of each trial type was similar in each decision and motor condition (Figure 2D).

249 To estimate the time at which subjects committed to their choice (decision time, DT) on each trial  
250 in the tokens task, we detected the time of movement onset, defining the subject’s reaction time  
251 (RT) and subtracted from it her/his mean sensory-motor delays (SM) estimated based on her/his  
252 reaction times in the same motor block of the delayed reach task performed the same day.  
253 Decision duration (DD) was computed as the duration between the DT and the first token jump.  
254 Equation 1 was then used to compute for each trial the success probability at the time of the  
255 decision (SP).

256 Calculation of subjects’ accuracy criterion at decision time relies on the available sensory  
257 evidence at that time. Because it is very unlikely that subjects can calculate Equation 1, we  
258 computed a simple “first-order” approximation of sensory evidence as the sum of log-likelihood  
259 ratios (SumLogLR) of individual token movements as follows (Cisek et al., 2009, page 11567,  
260 provides more details on this analysis):

$$SumLogLR(n) = \sum_{k=1}^n \log \frac{p(e_k|S)}{p(e_k|U)} \quad (2)$$

261 where  $p(e_k|S)$  is the likelihood of a token event  $e_k$  (a token jumping into either the selected or  
262 unselected target) during trials in which the selected target  $S$  is correct, and  $p(e_k|U)$  is its

## Impact of a demanding movement on decision-making

263 likelihood during trials in which the unselected target  $U$  is correct. The SumLogLR metric is thus  
264 proportional to the difference in the number of tokens that have moved in each circle before the  
265 moment of decision. To characterize the decision policy of a given subject in a given block of  
266 trials, we binned trials as a function of the total number of tokens that moved before the decision  
267 and calculated the average SumLogLR for each bin.

268 To quantify subjects' performance relative to the task objective, i.e. complete a given number of  
269 correct decisions, assuming they tried to complete each block as quickly as possible, we first  
270 calculated for correct and bad decisions the reward rate (RR), using a local definition (Haith et  
271 al., 2012; Thura et al., 2012) which corresponds to the expected number of correct choices per  
272 unit of time. This is computed as follows:

$$RR_n = \frac{SP_n}{DD_n + SM + MD_n + RD_n + ITI} \quad (3)$$

273 where  $SP_n$  is the probability that the choice made on trial  $n$  was correct,  $DD_n$  is the time taken to  
274 make the decision,  $SM$  is the sensorimotor delays (specific to each motor context but constant for  
275 a given session),  $MD_n$  is the movement duration,  $RD_n$  is the duration of the remaining token  
276 jumps after the target is reached, and  $ITI$  is the inter-trial interval (fixed at 1500ms). Then from  
277 the average reward rate computed in each motor block, we calculated the average number of  
278 correct choices per minute and deducted from it the time necessary to complete a given number  
279 of correct choices in each condition of interest.

280 Comparisons of decision duration, success probability, movement duration, peak velocity,  
281 accuracy, and block duration between conditions performed for each subject are statistically  
282 tested with Wilcoxon-Mann-Whitney (WMW, two-sided rank-sum) tests. The effect of motor  
283 condition on sensory evidence at decision time as a function of decision duration is statistically

## Impact of a demanding movement on decision-making

284 tested with analyses of covariance (ANCOVAs). For these analyses, very fast decisions made  
285 before token jump #4 are discarded. Decisions made before jump #4 were rare (see Thura, 2020)  
286 and success probability homogeneity (if subjects decide before token jump #4 it is likely because  
287 the first three tokens jumped into the same target) at that time makes data exclusion reasonable.  
288 The proportion of inadequate movements in small target conditions (small/short and small/long  
289 blocks) is statistically compared to the proportion of inadequate movements in big target  
290 conditions (big/short and big/long blocks) for each subject with chi-square tests. For all statistical  
291 tests, the significance level is set a 0.05.

292

## 293 RESULTS

### 294 *Effect of motor context on motor behavior in the tokens task*

295 As expected, the motor context in which decisions were reported strongly influenced subjects'  
296 movement properties and performance. First, we calculated the percentage of trials in which an  
297 inadequate movement was performed to express a choice, i.e. a movement exceeding 800ms (too  
298 slow) or failing to stop and maintain the position in the target within 800ms (inaccurate). In the  
299 first session, most subjects (18/20) performed significantly more inadequate movements in the  
300 small target (small/short and small/long blocks) condition compared to the big target (big/short  
301 and big/long blocks) condition (Chi-square tests,  $p < 0.05$ ). Movement "error" rates within blocks  
302 are the following across the population: small/long target blocks:  $18.8\% \pm 6.8$ ; small/short:  $5.5\%$   
303  $\pm 3.1$ ; big/long:  $4.5\% \pm 2.7$ ; big/short:  $1\% \pm 1.3$ . Despite an overall slight decrease, the same  
304 impact of motor constraint was observed on movement error rate during session #2: 19 out of 20  
305 subjects made more inadequate movements in the small target compared to the big target  
306 condition (Chi-square tests,  $p < 0.05$ ), with the following error rates in each of the four motor

## Impact of a demanding movement on decision-making

307 contexts: small/long target blocks: 16.7%  $\pm$ 4.5; small/short: 4.8%  $\pm$ 1.8; big/long: 2.35%  $\pm$ 1.5;  
308 big/short: 1.1%  $\pm$ 1.3). Figure 3A shows the dispersion of movement endpoints in one example  
309 subject who performed the tokens task in the four motor blocks. In this plot, correct and  
310 inadequate (too slow or inaccurate) movements trials are included. Confidence ellipses  
311 (containing 95% of all samples in each condition) largely extend outside of movement targets in  
312 small target trials, especially when targets are far from the starting center, whereas they almost  
313 entirely fit into movement targets in big target trials.

314 Then, we focused analyses on trials in which an adequate movement was performed to express a  
315 choice, irrespective of the outcome of that choice. As expected, reaching movement properties, in  
316 terms of velocity peak, duration, and endpoint “error” (the distance between target center and  
317 movement offset location) were affected by the motor context in which movements were  
318 executed. Figure 3B shows for the same representative subject the reaching velocity profiles in  
319 trials sorted as a function of the four motor blocks. Unsurprisingly, movement velocity was  
320 largely higher and duration longer in long target (dotted lines) compared to short target trials  
321 (solid lines), regardless of the size of the target. The size of the target also modulated movement  
322 speed and duration but to a lesser extent. Movements were indeed slightly faster and shorter  
323 when executed toward big targets (orange lines) compared to those executed toward small targets  
324 (blue lines).

325 This effect of motor context on movement properties was observed on the vast majority of  
326 subjects performing either the tokens or the delayed reach (DR) task. To simplify comparisons in  
327 the following analyses, we grouped trials depending on (1) target size, defining two conditions,  
328 small versus big target conditions, regardless of target distance from the starting circle, and (2)

## Impact of a demanding movement on decision-making

329 target distance from the starting circle, defining two other conditions, short versus long target  
330 conditions, regardless of target size.

331 First, most of the subjects reported decisions by making significantly faster (15 out of 20  
332 subjects, WMW test,  $p < 0.05$ ), shorter, in terms of duration (17 out of 20 subjects, WMW test,  
333  $p < 0.05$ ) and more dispersed (18/20, WMW test,  $p < 0.05$ ) movements in the big target compared  
334 to the small target condition (figure 4A). Second, all subjects reached long targets with  
335 significantly faster and longer movements compared to movements executed toward short targets  
336 (WMW test,  $p < 0.05$ , figure 4B, left and middle panels). In this distance contrast, we observed  
337 that endpoint distances from target center were not as consistently modulated as in the size  
338 contrast, being significantly larger for the long target compared to the short target condition in  
339 only 9 out of 20 subjects (WMW test,  $p < 0.05$ , figure 4B, right panel). The same influence of  
340 target characteristics on reaching velocity, duration, and accuracy was found in the DR task (not  
341 shown). Finally, the influence of target characteristics on movement parameters was similar in  
342 the two experimental sessions and the two decision blocks (slow and fast, not shown).

343 To summarize, manipulating the target characteristics in distinct blocks of trials successfully  
344 modulated reaching movement properties, encouraging subjects to either emphasize speed or  
345 accuracy to execute movements in these blocks to express their choices. In the following section,  
346 we assess whether or not these context-dependent adjustments of motor parameters influenced  
347 the decision policy leading to the actions executed to report choices.

### 348 *Effect of motor context on subjects' decision behavior*

349 To determine the potential impact of movement context on decision policy, we first analyzed  
350 subjects' decision duration (regardless of the decision outcome) by sorting trials depending on  
351 target characteristics, irrespective of the session and the decision condition (slow or fast).



## Impact of a demanding movement on decision-making

352 By first comparing decisions made in big (big/short and big/long) versus small (small/short and  
353 small/long) target trials, we found that decisions were overall shorter in the small target compared  
354 to the big target condition (1099 versus 1154ms). Importantly, the difference is significant for  
355 half of the population (WMW test,  $p < 0.05$ , figure 5A, left panel). Only one subject behaved the  
356 opposite way, making significantly faster choices when allowed to report them with fast, less  
357 accurate reaching movements. Importantly, we found virtually no difference between the average  
358 decision difficulties (quantified as success probability profiles, see Methods and figure 2D) in the  
359 two motor conditions, excluding a role of the sensory evidence experienced by the subjects in the  
360 difference of decision duration observed between small and big target contexts. Did this  
361 shortening of decision duration affect choice accuracy? To answer that question, we analyzed the  
362 amount of sensory evidence that subjects needed to commit to their choices (i.e. their accuracy  
363 criterion, computed as the sum of the log-likelihood ratios, see Methods), as a function of  
364 decision duration for the two motor conditions, small and big target trials (Figure 5A, middle  
365 panel). First, the level of sensory evidence that subjects required before committing to a choice  
366 decreased as a function of decision duration, irrespective of motor conditions (ANCOVA,  
367 SumLogLR, time effect,  $F_{(1,347)} = 164$ ,  $p < 0.0001$ ). This observation suggests that the more time  
368 is elapsing over the time course of a trial, the more decisions rely on a sensory-agnostic signal. In  
369 our previous studies as well as in others, this decreasing accuracy criterion is interpreted as a  
370 behavioral signature of an urgency-gating mechanism of decision-making, which in short  
371 describes the decision variable as the combination of sensory evidence with an urgency signal  
372 and the decision is made when the decision variable reaches a constant threshold (Cisek et al.,  
373 2009; Thura et al., 2012).

374 Importantly for the present report, we found that the accuracy criterion of subjects performing the  
375 tokens task in small target trials was significantly lower than in big target trials, for any decision

## Impact of a demanding movement on decision-making

376 made after token jump #3 (ANCOVA, SumLogLR, target size effect,  $F_{(1,347)} = 4.63$ ,  $p = 0.03$ ).

377 This indicates that subjects were more willing to tolerate less sensory evidence to make their  
378 choices in small target compared to big target trials. As a consequence, decisions were usually  
379 less likely to be correct in the small target compared to the big target context (Figure 5A, right  
380 panel). This decrease of success probability in small target trials was significant in 7 out of 10  
381 subjects showing a significant decrease of decision duration as a function of target size (WMW  
382 test,  $p < 0.05$ ).

383 We next compared decision durations in short versus long target trials, a contrast that strongly  
384 modulates movement speed of all subjects (Figure 4B, left panel). We found that the impact of  
385 target distance, and thus movement speed, on decision duration was less consistent at the  
386 population level compared to the impact of target size described above (Figure 5B, left panel).  
387 Indeed, we observed that 6 subjects made significantly longer decisions in the short target  
388 compared to the long target condition (WMW test,  $p < 0.05$ ), 4 subjects behaved the opposite way  
389 (WMW test,  $p < 0.05$ ), and the 10 remaining ones did not behave differently, in terms of decision  
390 duration, between the two motor conditions. We also found that target distance did not  
391 significantly influence the quantity of sensory information used by subjects to commit to their  
392 choice (ANCOVA, SumLogLR, target size effect,  $F_{(1,346)} = 0.13$ ,  $p = 0.72$ , Figure 5B, middle  
393 panel), and the success probability of these choices was only rarely significantly modulated as a  
394 function of target distance (Figure 5B, right panel).

395 We next analyzed the effect of target size and distance on subjects' reaction times (RT) in the  
396 delayed reach (DR) task. In the DR task, no volitional commitment needed to be made as subjects  
397 were instructed with both the correct target and when to execute their response (see Methods). In  
398 this task, we found that subjects' RTs were overall longer in small target compared to big target

## Impact of a demanding movement on decision-making

399 trials (375 versus 367ms), with a significant difference for 8 out of 20 subjects (WMW test,  
400  $p < 0.05$ ), and only one subject behaving significantly the opposite way (Figure 5C). Interestingly,  
401 we found a significant correlation between the modulation of decision duration by target size in  
402 the tokens task and the modulation of reaction time in the same conditions in the DR task. In  
403 other words, the more subjects expedited decisions in the small target condition of the tokens  
404 tasks, the more they slowed down their response initiation in the same condition in the DR task  
405 (Pearson correlation,  $r = -0.495$ ,  $p = 0.026$ , Figure 6). By contrast, reaction times were less  
406 homogeneously affected by the distance condition in the DR task. Four subjects reacted faster in  
407 short compared to long target blocks, and 3 subjects behaved the opposed way (WMW test,  
408  $p < 0.05$ , Figure 5D).

409 To assess whether the effect of target size on decision policy was dependent on the decision  
410 context, i.e. the slow or fast decision blocks of the tokens task, we computed subjects' decision  
411 duration, success probability, and sensory evidence at decision time for each of the two size  
412 conditions, separately for the two decision blocks. In a recent report (Thura, 2020), we describe  
413 in detail subjects' behavior in the two decision conditions. Quickly, the “slow” decision block of  
414 trials encourages slow and accurate decisions because the tokens that remain in the central  
415 decision circle after movement completion accelerate only a little compared to the pre-decision  
416 period (see Methods).

417 By contrast, in the “fast” block of trials, the remaining tokens accelerate a lot, allowing subjects  
418 to potentially save a lot of time by deciding quickly, permitting to eventually maximize their  
419 reward rate. In Thura, 2020 we showed that subjects behaved accordingly, making faster (1028 vs  
420 1229ms across subjects) and less accurate (0.87 versus 0.97) decisions in the fast block compared  
421 to the slow block of trials (see the average distributions of decision duration across subjects in the

## Impact of a demanding movement on decision-making

422 two decision blocks in Figure 7A,B). In the present report, we demonstrate that the impact of  
423 target size on decision policy, especially accuracy, is larger in the slow block than in the fast  
424 block of trials. Indeed, decision durations were significantly modulated by target size in 8 out of  
425 20 subjects performing the slow block whereas they were modulated in only 6 subjects  
426 performing the tokens task in the fast condition (WMW test,  $p < 0.05$ ). Moreover, the accuracy  
427 criterion was significantly higher for big target compared to small target trials in the slow block  
428 (ANCOVA, SumLogLR, size effect,  $F_{(1,345)} = 13.6$ ,  $p = 0.0003$ ) but not in the fast block ( $F_{(1,298)} =$   
429  $0.1$ ,  $p = 0.75$ , Figure 7A,B, left panels). As a consequence, success probability was strongly  
430 influenced by target size in the slow block (significantly modulated in 9 out of 20 subjects,  
431 WMW test,  $p < 0.05$ ) whereas effects were more balanced in the fast blocks (Figure 7A,B, right  
432 panels).

433 Next, we analyzed the effect of target size on decision policy depending on the level of  
434 experience of subjects in the tokens task. To do this, we computed subjects' decision duration,  
435 success probability, and sensory evidence at decision time for decisions made in the slow  
436 decision block for each of the two target size conditions, separately for the two experimental  
437 sessions. Overall, we found that the impact of the target size on decision policy did not strongly  
438 evolve with training. Decision durations were slightly more modulated by target size in the first  
439 session than in the second sessions (5/20 and 3/20 subjects with a significant effect of target size  
440 on decision duration in session #1 and #2, respectively; WMW test,  $p < 0.05$ ), but accuracy  
441 criterion (ANCOVA, SumLogLR, size effect,  $F_{(1,320)} = 2.5$ ,  $p = 0.1$  in session #1;  $F_{(1,330)} = 10.5$ ,  
442  $p = 0.0013$  in session #2) and to a lesser extent, success probability (4/20 and 5/20 subjects with a  
443 significant effect of target size on decision duration in session #1 and #2, respectively; WMW

## Impact of a demanding movement on decision-making

444 test,  $p < 0.05$ ) were more affected by target size in session #2 compared to session #1 (Figure  
445 7C,D).

446 Finally, we evaluated the impact of the faster and less accurate choices in the small target  
447 condition compared to the big target condition on subjects' performance in the tokens task.  
448 Because it has been shown that subjects seek to optimize their rate of correct responses rather  
449 than their absolute accuracy (Balci et al., 2011), performance is estimated as the duration that  
450 subjects needed to complete each motor block. Thus, by calculating the rate of reward and  
451 deducting from it the amount of time necessary to complete the different motor blocks in each  
452 session (see Methods), we found that this duration was significantly longer in the small target  
453 condition compared to the big target condition across subjects, regardless of the session  
454 performed, when subjects performed the tokens task in the slow decision block (WMW test,  $p =$   
455  $0.0013$ , Figure 8, left panel). By contrast, we found no significant difference in block duration  
456 between small and big target conditions in the fast decision block of trials (WMW test,  $p = 0.11$ ,  
457 Figure 8, right panel).

458

459

## DISCUSSION

460 In this study, we assessed whether the motor context in which perceptual decisions between  
461 actions are made influences human subjects' decision strategy, as predicted by the recently  
462 proposed "shared regulation" hypothesis (Thura et al., 2014). This model conceives decision and  
463 action as a continuum, regulated by unspecific signals. As a consequence, a motor context  
464 favoring vigorous movements should be preceded by fast decisions because of the activation of  
465 one unique invigoration signal possibly computed in the basal ganglia (Cisek and Thura, 2018).  
466 We found that motor context indeed often influences decision-making but contrary to the

## Impact of a demanding movement on decision-making

467 prediction of the shared regulation hypothesis, decisions preceding slow and accurate actions  
468 were faster, rather than slower, compared to decisions made in blocks allowing more vigorous  
469 and less accurate actions.

470 In the present task, the action vigor (indicated by movement speed and duration) is assumed to be  
471 determined depending on the speed-accuracy trade-off of each motor condition. However,  
472 motivation factors, such as the movement energetic cost, may have contributed to shape action  
473 vigor as well (Mazzoni et al., 2007). With the present design, we cannot disentangle the  
474 contribution of the accuracy and energy costs on vigor definition, the slower movements  
475 executed toward the small targets being also less energetically costly. However, if we assume that  
476 the less energetically costly movements should increase the subjects' implicit motivation to  
477 decide and act (Mazzoni et al., 2007), those movements should be executed faster than the  
478 effortful ones. Yet, our data indicate the opposite results. We thus believe that the accuracy  
479 requirement is the main factor that determined movement vigor in our experiment.

### 480 *Motor costs influence motor and perceptual decision-making*

481 The present results first add to the many recent observations that challenge the classic view of  
482 behavior organization, inherited from cognitive psychology, in which perception, decision, and  
483 action are considered as temporally separate and serial processes (Pylyshyn, 1984). Indeed, in  
484 ecological scenarios, sensory or value-based decisions are very often expressed by actions that  
485 are themselves associated with risks and costs. For instance, a monkey deciding between reaching  
486 toward a grape or a nut may prefer the nut but time and energy expenditure associated with  
487 opening its shell may rather encourage him to go for the grape. Because it has been extensively  
488 demonstrated that the brain tends to control behavior in such a way that the expected value of a  
489 choice is maximized while all types of cost are minimized (Neumann and Morgenstern, 1944;

## Impact of a demanding movement on decision-making

490 Todorov and Jordan, 2002; Gold and Shadlen, 2007; Christopoulos and Schrater, 2015;  
491 Christopoulos et al., 2015; Diamond et al., 2017), any potentially penalizing factor, including  
492 motor costs, should influence the perceptual judgment leading to a potential reward.

493 In the past decade, several studies have demonstrated that motor costs influence decision-making  
494 when choices only rely on movement properties (i.e. motor decisions). Cos and colleagues  
495 showed that when humans make rapid choices between reaching actions, they tend to choose the  
496 one that carries the lowest biomechanical cost (Cos et al., 2011, 2014). Morel and colleagues  
497 found that biomechanics affects action selection too, but among duration, amplitude, direction  
498 and force, they observed that movement duration is perceived as the greatest cost by subjects  
499 (Morel et al., 2017). Finally, Michalski and colleagues observed that movement amplitude and  
500 direction influence the probability of switching from one ongoing movement to another in a  
501 common real-life scenario where one has to decide while already acting (Michalski et al., 2020).

502 Other work addressed the effects of motor costs on decision-making beyond purely motor  
503 choices, i.e. when the decision primarily relies on perceptual or value information, as in the  
504 present work. In three of these experiments using the random dots motion discrimination task,  
505 data indicate an effect of motor constraints on non-motor decision-making. Burk and colleagues  
506 demonstrated that physical effort affects the proportion of changes of mind made by subjects  
507 during the deliberation period: the more the change of mind requires a significant energetic cost,  
508 the less subjects are willing to perform it (Burk et al., 2014). Another study showed that  
509 asymmetric biomechanical cost biases perceptual decisions, with subjects more systematically  
510 choosing targets associated with movements of lower cost, even if these choices were detrimental  
511 to accuracy (Marcos et al., 2015). In agreement with this observation, Hagura and colleagues  
512 demonstrated that motion discrimination is influenced by the physical resistance applied to the

## Impact of a demanding movement on decision-making

513 response. Intriguingly, they showed that motor costs also bias vocally-expressed judgments,  
514 suggesting that actions changed how subjects perceived the stimuli themselves (Hagura et al.,  
515 2017). It is important to note that in these three studies, each of the two potential targets was  
516 assigned a specific motor cost during a given choice. By contrast, in the present work, the two  
517 targets were always associated with the same motor cost, and that cost was varied between blocks  
518 of trials. The present report is thus to our knowledge the first to show that the motor context in  
519 which a movement is performed influences the strategy of subjects during decision-making.

### 520 *A flexible mechanism for regulating decision and movement durations*

521 Decisions about actions typically include a period of deliberation that ends with the commitment  
522 to a choice, which then leads to the overt expression of that choice through action execution, at  
523 the end of which the reward can be at last consumed. Because decision and action processes are  
524 so inextricably linked, it is natural to imagine that they could at least partly share operating  
525 principles to maximize the utility of behavior. Decision and action could indeed be considered as  
526 a continuum during which regulation signals would affect both processes agnostically, in a  
527 unified manner. In agreement with this hypothesis, it has been proposed that movement selection,  
528 preparation, and execution are parameterized following economical rules, varying depending on  
529 utility estimation: high valued options lead to faster reaction times and movement speed, and  
530 high-perceived effort discount option's value, leading to slower reaction and longer movements  
531 (Kawagoe et al., 1998; Wickler et al., 2000; Shadmehr et al., 2010, 2016, 2019; Haith et al.,  
532 2012; Choi et al., 2014; Morel et al., 2017; Reppert et al., 2018; Summerside et al., 2018; Yoon et  
533 al., 2018; Revol et al., 2019).

534 Our previous results support this hypothesis of a coordination between decision and action  
535 durations during behavior. For instance, within fixed decision and motor contexts, both humans



## Impact of a demanding movement on decision-making

536 and monkeys shorten their movement duration in trials in which decision duration is prolonged,  
537 as if extended deliberation duration was compensated by increasing the action speed so that the  
538 next opportunity can be encountered more quickly. Between decision contexts, choices made in a  
539 fast speed-accuracy trade-off regime are usually followed by faster movements compared to  
540 those made in a regime encouraging slow and accurate choices (Thura et al., 2014; Thura, 2020).  
541 Altogether, these observations indicate that the level of urgency at which a decision is made  
542 directly influences movement vigor, suggesting that decision and movement durations are  
543 determined by a global decision urgency/movement vigor signal that invigorates behavior in  
544 order to control reward rate (Cisek and Thura, 2018; Carland et al., 2019). However, a missing  
545 test of the shared regulation hypothesis required to vary the motor context in which a decision is  
546 made and assess whether or not a motor context permitting execution of vigorous movements to  
547 express choices leads to faster decisions compared to the same difficult decisions made in a  
548 demanding motor context, imposing slow and accurate movements. Contrary to this prediction,  
549 we did not observe a robust and consistent effect of movement speed per se on decision duration  
550 and accuracy (by comparing short versus long target conditions, Figure 5B). Instead, data  
551 indicate that target size imposes a motor accuracy cost that is tackled by some subjects by  
552 shortening the deliberation period (Figure 5A) so that more time is available to prepare the  
553 following movement execution. This interpretation is supported by a post-experiment interview  
554 during which most of the participants declared having consciously expedited and thus  
555 “sacrificed” their decisions to better prepare action execution in small target trials.

556 One critical assumption in this experiment is that action towards the smaller targets requires less  
557 vigor compared to the action executed toward large targets. However, an alternative  
558 interpretation would state that because small targets impose more preparation time (reaction

## Impact of a demanding movement on decision-making

559 times are overall longer for small targets than for big targets in the DR task, figure 5C), a  
560 potential preparation-related urgency would have more time to increase in the small target blocks  
561 compared to the big target blocks, leading to movements initiated under higher urgency in the  
562 small blocks compare to the big blocks. The slower velocity and longer movement duration  
563 observed in the small blocks (Figure 4A for the tokens task) would then be explained by possible  
564 different systems for governing action preparation and execution (e.g. Haith et al., 2016).  
565 However, we do not believe that a putative preparation-related urgency signal could explain our  
566 results because no influence of this urgency is expected at the beginning of the trial and during  
567 the deliberation process. Instead, the preparation-related urgency level might differ between the  
568 blocks only after commitment, i.e. during movement preparation.

569 Thus, the present results more likely demonstrate that an unconditional and unidirectional  
570 relationship between action vigor and decision duration, as predicted by the shared regulation  
571 hypothesis, is absent. Instead, our results claim for a flexible mechanism in which decision and  
572 action durations are regulated by independent, yet interacting, decision urgency and movement  
573 vigor signals. Such flexibility is certainly advantageous given the inherent complexity of the  
574 many variables interrelationships at play during goal-directed behavior, where no single decision  
575 policy is guaranteed to maximize the reward rate across all contexts.

576 Flexibility between decision-making and action execution is well illustrated by the relationship  
577 between the effect of target size on decision duration in the tokens task and the effect of target  
578 size on reaction time in the delayed reach (DR) task. The significant correlation (Figure 6)  
579 indicates that subjects who are slower to initiate a movement in the small target trials of the DR  
580 task are also the subjects who adjust their decision policy the most in these difficult trials in the  
581 tokens task. The former result is consistent with data suggesting that effortful movements

## Impact of a demanding movement on decision-making

582 discount reward value, thus motivation, delaying the initiation of movements (Mazzoni et al.,  
583 2007; Summerside et al., 2018; Shadmehr et al., 2019). This relationship thus suggests that  
584 economic principles governing behavior utility in non-decision tasks extend to decision-making.  
585 It also indicates that when the task difficulty mainly relies on movement execution, as in the DR  
586 task, movement effort slows down reaction times whereas when task difficulty is shared between  
587 decision and action, as in the tokens task, movement effort influences the decision process in an  
588 opposite way. What could be the relevance of this intriguing behavior in terms of performance?

### 589 *Impact of a demanding movement on reward rate*

590 The present data indicate that movement accuracy requirements, more than speed or duration,  
591 forced some subjects to hasten their decisions. It seems that they took advantage of the  
592 potentially long deliberation period permitted in the task (up to 3s) to sometimes shorten their  
593 judgment in order to focus on the following movement execution. Interestingly, such adjustment  
594 only occurred in blocks of trials in which decisions were encouraged to be conservative (“slow”  
595 decision blocks, Figure 7). Indeed, the large and very profitable, in terms of reward rate,  
596 shortening of decision durations observed in the “fast” decision blocks (Figure 8) probably  
597 constrained decision policy too much, preventing any other adjustments of behavior. It is also  
598 important to remember that in the tokens task, deciding more quickly does not provide additional  
599 time to execute the movement, the maximum movement duration being fixed at 800ms regardless  
600 of subjects’ reach onset timing. How then can one explain this suboptimal strategy? One  
601 possibility is that our limited cognitive and motor resources imposed a necessary trade-off  
602 between decision and action when task constraints were too demanding (Wickens, 2002). In this  
603 view, subjects had to choose between allocating resources on decision-making while taking the  
604 risk of producing inaccurate movements or rather sacrificing decision-making to presumably

## Impact of a demanding movement on decision-making

605 better prepare and execute their movements. Knowing that in ecological situations as in the  
606 present task, a movement usually follows the decision, it is possible that subjects gave priority to  
607 the action process considering that movement failure would prevent reward acquisition even if  
608 the decision was correct. Although it may be advantageous in terms of reward rate to decide very  
609 quickly while sacrificing a little bit of precision (see equation 3), as observed when humans and  
610 monkeys decide faster in the fast compared to the slow decision block of trials (Figure 8 and  
611 Thura et al., 2014; Thura, 2020), our results show however that the strategy consisting of  
612 sacrificing decision accuracy to execute accurate movements led to a drop of reward rate  
613 compared to a condition in which such adjustment was not necessary. This is probably because in  
614 small target trials, the probability of choosing the correct target decreased, even if the amount of  
615 time saved during the deliberation period compensated the longer movements made in this  
616 condition (Figure 4).

### 617 *Possible neurophysiological origin of the decision and action regulation mechanism*

618 The interaction between the decision and action regulations provides a clue to the neural origins  
619 of the signals implicated in this mechanism. Interacting decision urgency and movement vigor  
620 signals would be expected to originate from a region that projects to a wide range of cortical  
621 areas to influence both decision-making and action execution. In this respect, the basal ganglia  
622 (BG) provide a natural candidate. The BG have long been functionally associated with the  
623 regulation of motivated behavior and reinforcement learning for maximizing reward (Graybiel,  
624 2005; Frank, 2011), and multiple lines of neuropsychological, neurological and  
625 neurophysiological evidence suggest that effort expenditure and movement vigor are largely  
626 under the control of activity within a variety of BG structures, including the striatum, substantia  
627 nigra, ventral pallidum, and the globus pallidus (Mazzoni et al., 2007; Turner and Desmurget,

## Impact of a demanding movement on decision-making

628 2010; Rueda-Orozco and Robbe, 2015; Dudman and Krakauer, 2016; Thura and Cisek, 2017; da  
629 Silva et al., 2018; Yttri and Dudman, 2018; Carland et al., 2019; Fobbs et al., 2020). All these  
630 studies along with results from the present report suggest a mechanism in which different  
631 populations of cells, located in the BG output nuclei, vary their activity to adjust both decision  
632 and motor durations under specific circumstances, in order to control the rate of reward. Future  
633 experiments designed to record the activity of individual BG cells during decision-making  
634 between actions in different decision and motor contexts should allow us to better understand the  
635 neural correlates of this regulation mechanism.

### 636 *Limitations*

637 A limitation of the present study, as often in investigations of primate cognition and behavior,  
638 relates to the between-subject variability of the results. The average decision duration ranges  
639 from ~700ms to about 1600ms depending on subjects (Figure 5), even though participants faced  
640 the same trials under identical conditions. This indicates individual “traits” of decision behavior.  
641 Similarly, a subgroup of four subjects was more vigorous than the others to execute their  
642 movements (Figure 4). While revealing probable unaddressed phenomena, these multiple levels  
643 of variability are still compatible with a flexible regulation mechanism of decision and action  
644 durations that would be idiosyncratic in nature. Another limitation concerns the absence of  
645 analysis of decision data in inaccurate or slow movement trials for methodology reasons. In the  
646 present report, we show that a difficult movement is often preceded by a fast and inaccurate  
647 decision, but this occurs when movements are properly executed. It is possible that subjects  
648 sometimes allocated their attention on the decision process, leading in that case to a “sacrifice” of  
649 motor control, resulting in failed movements. Further experiments or analyses are needed to

## Impact of a demanding movement on decision-making

650 reveal which of the two processes, the decision or the action, is typically prioritized by  
651 participants in this kind of demanding goal-directed behavior.

652

653

## ACKNOWLEDGMENTS

654 The authors wish to thank Sonia Alouche and Jean-Louis Borach for effective administrative  
655 assistance, Paul Cisek for his contribution in setting up the software environment, Frédéric  
656 Volland for his expertise during the technical preparation of this experiment, and Martine  
657 Meunier for helpful suggestions on the manuscript.

## Impact of a demanding movement on decision-making

658 **FIGURE CAPTIONS**

659

660 **Figure 1: The “shared regulation” hypothesis.** A. Simplified hypothetical mechanism of a

661 shared regulation of decision and movement durations by one unique invigoration (decision

662 urgency/movement vigor) signal, possibly computed in the basal ganglia (Thura et al., 2014;

663 Thura and Cisek, 2017). The thick black lines illustrate the manipulation of the motor context,

664 tested in the present study, leading to the modulation of the urgency/vigor signal. B. The shared

665 regulation hypothesis makes a simple prediction regarding the effect of the motor context in

666 which a decision is made on the duration of that decision: if a context encourages execution of

667 vigorous (faster, shorter) movements (orange) to report choices, then the urgency level in this

668 context should be raised compared to another context in which movements need to be less

669 vigorous but more accurate (blue). As a consequence, equally difficult decisions made in the

670 vigorous block of trials should be on average shorter than those made in the block encouraging

671 slow and accurate movements.

672

673 **Figure 2: Apparatus, experimental design, and conditions.** A. Experimental apparatus. B.

674 Time course of a trial in the tokens task. C. Motor conditions, i.e. movement target size and

675 distance combinations. In distinct blocks of trials, both lateral targets could be either small and

676 located close to the starting circle (black), small and located far from the starting circle, big and

677 located close to the starting circle or big and located far from the starting circle. D. Average

678 success probability profiles of trials experienced by subjects in each of the four motor conditions.

679

680 **Figure 3: Motor behavior in one example subject.** A. Panel shows the motor visual display

681 depicted in Figure 2, along with shaded ellipses illustrating for each motor condition and side

## Impact of a demanding movement on decision-making

682 with respect to the start circle (black) the dispersion (an iso-contour of the Gaussian distribution)  
683 of one example subject reaching endpoints in the tokens task. Each ellipse contains 95% of the  
684 data in each condition, and trials include correct and inadequate (too slow or inaccurate)  
685 movements executed in the two sessions and the two decision conditions (slow and fast). B.  
686 Reach velocity profiles of the same subject in the four motor conditions. Same color/style  
687 convention as in A. Only adequate movements are included.

688  
689 **Figure 4: Effect of motor context on population motor behavior.** A. Average reaching  
690 movement peak velocity (left), duration (middle) and target center-endpoint distance (right) of  
691 each subject during big target (big/short and big/long blocks, x-axis) and small target (small/short  
692 and small/long blocks, y-axis) conditions performed in the tokens task. Green (magenta) pluses  
693 indicate the mean and SE for subjects for whom data is larger (smaller) in the big target condition  
694 compared to the small target condition and the difference was significant (WMW test,  $p < 0.05$ ).  
695 Data include trials collected from both sessions #1 and #2, in both the slow and fast decision  
696 blocks. B. Same as A for trials executed in the long target (small/long and big/long blocks, x-  
697 axis) versus the short target (small/short and big/short blocks, y-axis) condition.

698  
699 **Figure 5 : Effect of motor context on decision behavior.** A. Left: Average decision duration of  
700 each subject during big (x-axis) and small (y-axis) target conditions performed in the tokens task.  
701 Same convention as in Figure 4. Middle: Average ( $\pm$  SE) evidence at decision time across  
702 subjects as a function of decision duration in the small (blue) and the big (orange) target  
703 conditions of the tokens task. Right: Mean success probability of each subject during big (x-axis)  
704 and small (y-axis) target conditions performed in the tokens task. Same convention as in Figure 4.



## Impact of a demanding movement on decision-making

705 Data include trials collected from both sessions #1 and #2, in both the slow and fast decision  
706 blocks. B. Same as A for trials executed in the long versus short target conditions. C. Average  
707 reaction time of each subject during big (x-axis) and small (y-axis) target conditions performed in  
708 the delayed reach task. D. Same as C for trials executed in the long (x-axis) versus the short (y-  
709 axis) target condition.

710  
711 **Figure 6: Relationship between the effect of motor context on the decision and instructed**  
712 **tasks.** Left: Correlation between the difference of decision duration in small versus big target  
713 conditions in the tokens task (x-axis) and the difference of reaction time in the same conditions in  
714 the delayed reach task (y-axis). Each dot shows data from one individual subject. Right: Same as  
715 Left for the distance contrast (short versus long target conditions).

716  
717 **Figure 7: Effect of motor context on decision accuracy depending on decision context and**  
718 **experience.** A. Left: Average ( $\pm$  SE) evidence at decision time across subjects as a function of  
719 decision duration in small (blue) and big (orange) target conditions performed in the “slow”  
720 decision block of the tokens task. The black line below shows the average distribution of decision  
721 duration across subjects in the slow block. Right: Average success probability of each subject  
722 during big (x-axis) and small (y-axis) target conditions performed in the slow decision block of  
723 the tokens task. Data from both sessions #1 and #2 are included. Same convention as in Figure 4.  
724 B. Same as A for decisions made in the “fast” decision block of the tokens task. C. Same as A for  
725 decisions made in the first session, including only slow decision blocks. D. Same as C for  
726 decisions made during the second session.

727

## Impact of a demanding movement on decision-making

728 **Figure 8: Influence of target size on the expected duration of blocks.** Bars show the average  
729 expected time necessary to complete a block of 80 trials, computed based on reward rate in each  
730 condition, in the small (blue) and big (orange) target block across subjects and sessions, in the  
731 slow (left) and fast (right) decision block of trials. Dots illustrate individual data.  
732

## Impact of a demanding movement on decision-making

### REFERENCES

- 733
- 734 Balci F, Simen P, Niyogi R, Saxe A, Hughes JA, Holmes P, Cohen JD (2011) Acquisition of  
735 decision making criteria: reward rate ultimately beats accuracy. *Atten Percept Psychophys*  
736 73:640–657.
- 737 Bogacz R, Hu PT, Holmes PJ, Cohen JD (2010) Do humans produce the speed–accuracy trade-  
738 off that maximizes reward rate? *Quarterly Journal of Experimental Psychology* 63:863–  
739 891.
- 740 Burk D, Ingram JN, Franklin DW, Shadlen MN, Wolpert DM (2014) Motor Effort Alters  
741 Changes of Mind in Sensorimotor Decision Making Kiebel S, ed. *PLoS ONE* 9:e92681.
- 742 Carland MA, Thura D, Cisek P (2019) The Urge to Decide and Act: Implications for Brain  
743 Function and Dysfunction. *Neuroscientist*:107385841984155.
- 744 Choi JES, Vaswani PA, Shadmehr R (2014) Vigor of Movements and the Cost of Time in  
745 Decision Making. *Journal of Neuroscience* 34:1212–1223.
- 746 Christopoulos V, Bonaiuto J, Andersen RA (2015) A biologically plausible computational theory  
747 for value integration and action selection in decisions with competing alternatives. *PLoS*  
748 *Comput Biol* 11:e1004104.
- 749 Christopoulos V, Schrater PR (2015) Dynamic Integration of Value Information into a Common  
750 Probability Currency as a Theory for Flexible Decision Making. *PLoS Comput Biol*  
751 11:e1004402.

## Impact of a demanding movement on decision-making

- 752 Churchland AK, Kiani R, Shadlen MN (2008) Decision-making with multiple alternatives. Nat  
753 Neurosci 11:693–702.
- 754 Cisek P, Puskas GA, El-Murr S (2009) Decisions in Changing Conditions: The Urgency-Gating  
755 Model. Journal of Neuroscience 29:11560–11571.
- 756 Cisek P, Thura D (2018) Neural circuits for action selection. In: Reach-to-grasp behavior: Brain,  
757 behavior, and modelling across the life span, Daniela Corbetta and Marco Santello., pp  
758 91–118 Frontiers of developmental science. Taylor & Francis Group.
- 759 Cos I, Bélanger N, Cisek P (2011) The influence of predicted arm biomechanics on decision  
760 making. Journal of Neurophysiology 105:3022–3033.
- 761 Cos I, Duque J, Cisek P (2014) Rapid prediction of biomechanical costs during action decisions.  
762 Journal of Neurophysiology 112:1256–1266.
- 763 Cos I, Medleg F, Cisek P (2012) The modulatory influence of end-point controllability on  
764 decisions between actions. Journal of Neurophysiology 108:1764–1780.
- 765 da Silva JA, Tecuapetla F, Paixão V, Costa RM (2018) Dopamine neuron activity before action  
766 initiation gates and invigorates future movements. Nature 554:244–248.
- 767 Diamond JS, Wolpert DM, Flanagan JR (2017) Rapid target foraging with reach or gaze: The  
768 hand looks further ahead than the eye. PLoS Comput Biol 13:e1005504.
- 769 Ditterich J (2006) Evidence for time-variant decision making. European Journal of Neuroscience  
770 24:3628–3641.

## Impact of a demanding movement on decision-making

- 771 Dudman JT, Krakauer JW (2016) The basal ganglia: from motor commands to the control of  
772 vigor. *Current Opinion in Neurobiology* 37:158–166.
- 773 Fobbs WC, Bariselli S, Licholai JA, Miyazaki NL, Matikainen-Ankney BA, Creed MC, Kravitz  
774 AV (2020) Continuous Representations of Speed by Striatal Medium Spiny Neurons. *J*  
775 *Neurosci* 40:1679–1688.
- 776 Frank MJ (2011) Computational models of motivated action selection in corticostriatal circuits.  
777 *Current Opinion in Neurobiology* 21:381–386.
- 778 Gold JI, Shadlen MN (2007) The Neural Basis of Decision Making. *Annu Rev Neurosci* 30:535–  
779 574.
- 780 Graybiel AM (2005) The basal ganglia: learning new tricks and loving it. *Current Opinion in*  
781 *Neurobiology* 15:638–644.
- 782 Hagura N, Haggard P, Diedrichsen J (2017) Perceptual decisions are biased by the cost to act.  
783 *eLife* 6:e18422.
- 784 Haith AM, Pakpoor J, Krakauer JW (2016) Independence of Movement Preparation and  
785 Movement Initiation. *J Neurosci* 36:3007–3015.
- 786 Haith AM, Reppert TR, Shadmehr R (2012) Evidence for Hyperbolic Temporal Discounting of  
787 Reward in Control of Movements. *Journal of Neuroscience* 32:11727–11736.
- 788 Kawagoe R, Takikawa Y, Hikosaka O (1998) Expectation of reward modulates cognitive signals  
789 in the basal ganglia. *Nat Neurosci* 1:411–416.

## Impact of a demanding movement on decision-making

- 790 Kira S, Yang T, Shadlen MN (2015) A Neural Implementation of Wald's Sequential Probability  
791 Ratio Test. *Neuron* 85:861–873.
- 792 Malhotra G, Leslie DS, Ludwig CJH, Bogacz R (2017) Overcoming indecision by changing the  
793 decision boundary. *Journal of Experimental Psychology: General* 146:776–805.
- 794 Malhotra G, Leslie DS, Ludwig CJH, Bogacz R (2018) Time-varying decision boundaries:  
795 insights from optimality analysis. *Psychon Bull Rev* 25:971–996.
- 796 Marcos E, Cos I, Girard B, Verschure PFMJ (2015) Motor Cost Influences Perceptual Decisions  
797 Gribble PL, ed. *PLoS ONE* 10:e0144841.
- 798 Mazzoni P, Hristova A, Krakauer JW (2007) Why Don't We Move Faster? Parkinson's Disease,  
799 Movement Vigor, and Implicit Motivation. *Journal of Neuroscience* 27:7105–7116.
- 800 Michalski J, Green AM, Cisek P (2020) Reaching decisions during ongoing movements. *Journal*  
801 *of Neurophysiology* 123:1090–1102.
- 802 Morel P, Ulbrich P, Gail A (2017) What makes a reach movement effortful? Physical effort  
803 discounting supports common minimization principles in decision making and motor  
804 control Rushworth M, ed. *PLoS Biol* 15:e2001323.
- 805 Murphy PR, Boonstra E, Nieuwenhuis S (2016) Global gain modulation generates time-  
806 dependent urgency during perceptual choice in humans. *Nat Commun* 7:13526.
- 807 Myerson J, Green L (1995) Discounting of delayed rewards: models of individual choice. *Journal*  
808 *of the Experimental Analysis of Behavior*:263–276.

## Impact of a demanding movement on decision-making

- 809 Neumann J von, Morgenstern O (1944) *Theory of Games and Economic Behavior*, Princeton  
810 University Press.
- 811 Reppert TR, Rigas I, Herzfeld DJ, Sedaghat-Nejad E, Komogortsev O, Shadmehr R (2018)  
812 Movement vigor as a traitlike attribute of individuality. *Journal of Neurophysiology*  
813 120:741–757.
- 814 Revol P, Collette S, Boulot Z, Foncelle A, Niki C, Thura D, Imai A, Jacquin-Courtois S, Cabanac  
815 M, Osiurak F, Rossetti Y (2019) Thirst for Intention? Grasping a Glass Is a Thirst-  
816 Controlled Action. *Front Psychol* 10:1248.
- 817 Rueda-Orozco PE, Robbe D (2015) The striatum multiplexes contextual and kinematic  
818 information to constrain motor habits execution. *Nat Neurosci* 18:453–460.
- 819 Shadmehr R, Huang HJ, Ahmed AA (2016) A Representation of Effort in Decision-Making and  
820 Motor Control. *Current Biology* 26:1929–1934.
- 821 Shadmehr R, Orban de Xivry JJ, Xu-Wilson M, Shih T-Y (2010) Temporal Discounting of  
822 Reward and the Cost of Time in Motor Control. *Journal of Neuroscience* 30:10507–  
823 10516.
- 824 Shadmehr R, Reppert TR, Summerside EM, Yoon T, Ahmed AA (2019) Movement Vigor as a  
825 Reflection of Subjective Economic Utility. *Trends in Neurosciences* 42:323–336.
- 826 Standage D, You H, Wang D-H, Dorris MC (2011) Gain Modulation by an Urgency Signal  
827 Controls the Speed–Accuracy Trade-Off in a Network Model of a Cortical Decision  
828 Circuit. *Front Comput Neurosci* 5 Available at:

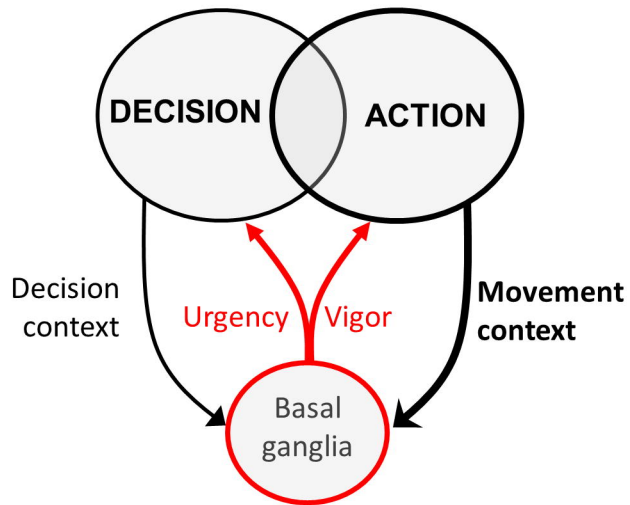
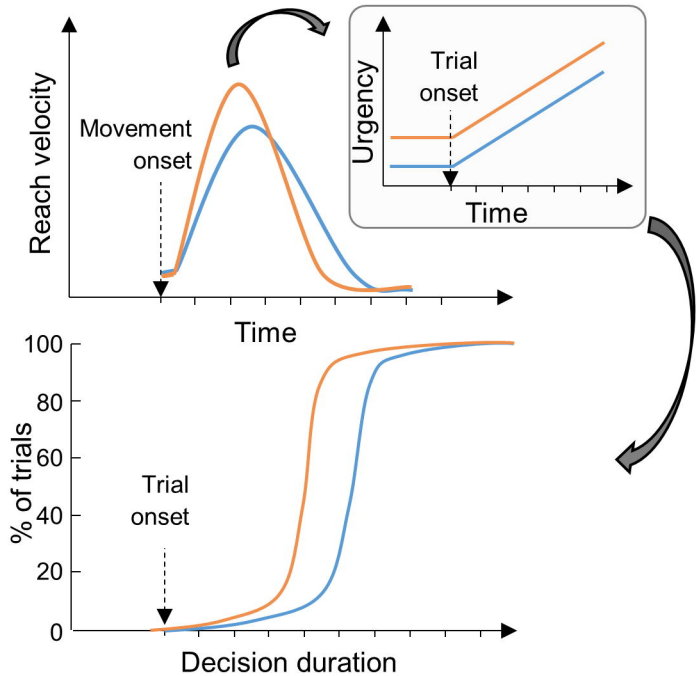
## Impact of a demanding movement on decision-making

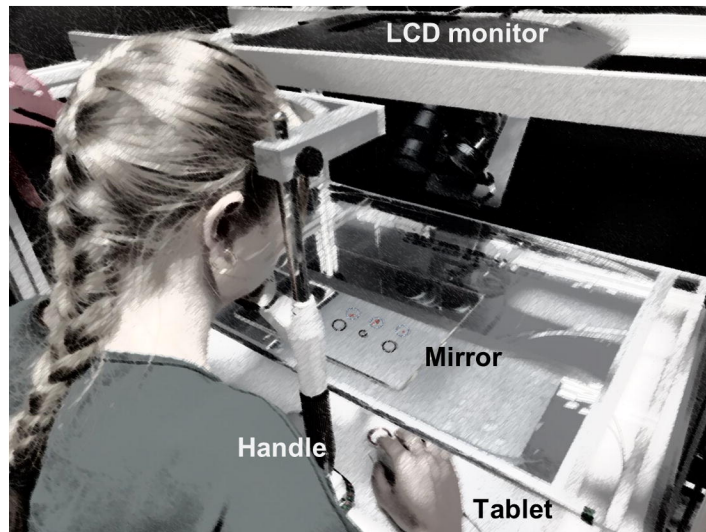
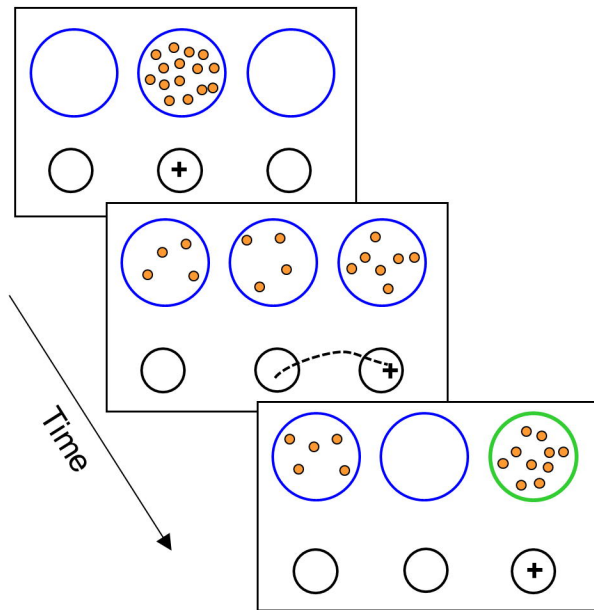
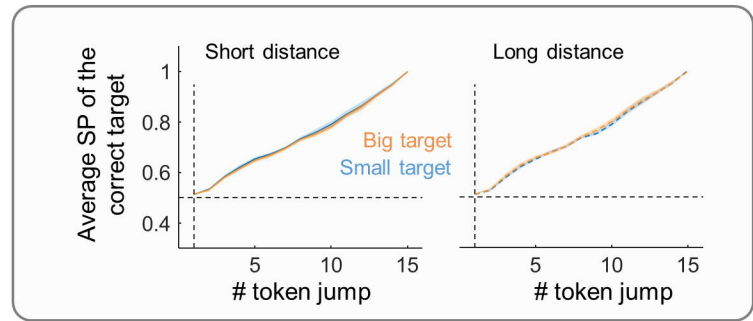
- 829 <http://journal.frontiersin.org/article/10.3389/fncom.2011.00007/abstract> [Accessed  
830 September 9, 2019].
- 831 Steinemann NA, O’Connell RG, Kelly SP (2018) Decisions are expedited through multiple  
832 neural adjustments spanning the sensorimotor hierarchy. *Nat Commun* 9:3627.
- 833 Summerside EM, Shadmehr R, Ahmed AA (2018) Vigor of reaching movements: reward  
834 discounts the cost of effort. *Journal of Neurophysiology* 119:2347–2357.
- 835 Thura D (2020) Decision urgency invigorates movement in humans. *Behavioural Brain Research*  
836 382:112477.
- 837 Thura D, Beauregard-Racine J, Fradet C-W, Cisek P (2012) Decision making by urgency gating:  
838 theory and experimental support. *J Neurophysiol* 108:2912–2930.
- 839 Thura D, Cisek P (2014) Deliberation and commitment in the premotor and primary motor cortex  
840 during dynamic decision making. *Neuron* 81:1401–1416.
- 841 Thura D, Cisek P (2016) Modulation of Premotor and Primary Motor Cortical Activity during  
842 Volitional Adjustments of Speed-Accuracy Trade-Offs. *J Neurosci* 36:938–956.
- 843 Thura D, Cisek P (2017) The Basal Ganglia Do Not Select Reach Targets but Control the  
844 Urgency of Commitment. *Neuron* 95:1160-1170.e5.
- 845 Thura D, Cos I, Trung J, Cisek P (2014) Context-dependent urgency influences speed-accuracy  
846 trade-offs in decision-making and movement execution. *J Neurosci* 34:16442–16454.
- 847 Todorov E, Jordan MI (2002) Optimal feedback control as a theory of motor coordination. *Nat*  
848 *Neurosci* 5:1226–1235.



## Impact of a demanding movement on decision-making

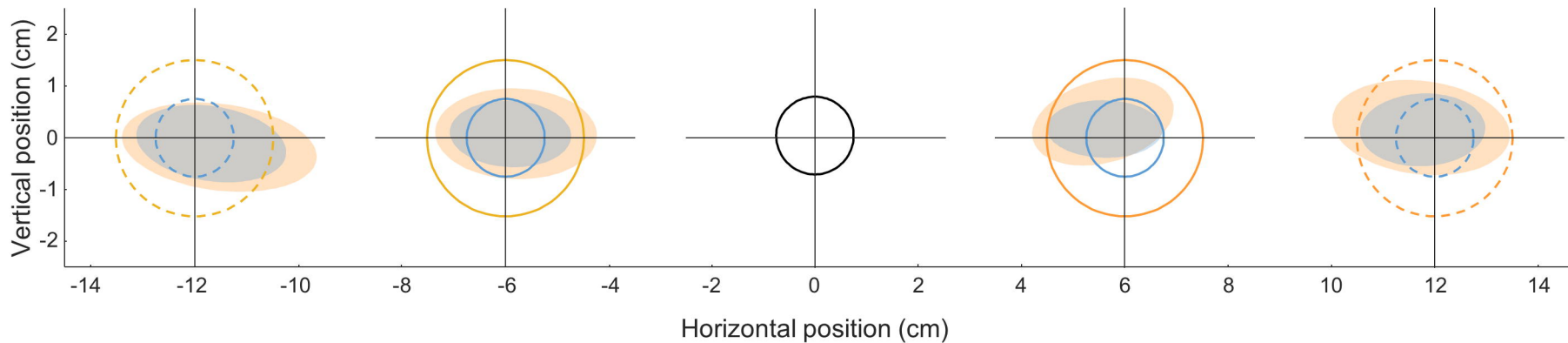
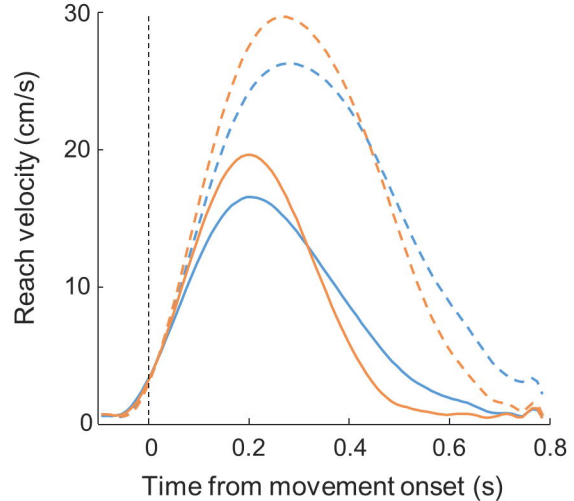
- 849 Turner RS, Desmurget M (2010) Basal ganglia contributions to motor control: a vigorous tutor.  
850 *Current Opinion in Neurobiology* 20:704–716.
- 851 Wickens CD (2002) Multiple resources and performance prediction. *Theoretical Issues in*  
852 *Ergonomics Science* 3:159–177.
- 853 Wickler SJ, Hoyt DF, Cogger EA, Hirschbein MH (2000) Preferred speed and cost of transport.  
854 *Journal of Experimental Biology*:2195–2200.
- 855 Yoon T, Geary RB, Ahmed AA, Shadmehr R (2018) Control of movement vigor and decision  
856 making during foraging. *Proc Natl Acad Sci USA* 115:E10476–E10485.
- 857 Yttri EA, Dudman JT (2018) A Proposed Circuit Computation in Basal Ganglia: History-  
858 Dependent Gain: Proposed Circuit Computation in Basal Ganglia. *Mov Disord* 33:704–  
859 716.
- 860

**A****B**

**A****B****C****D**

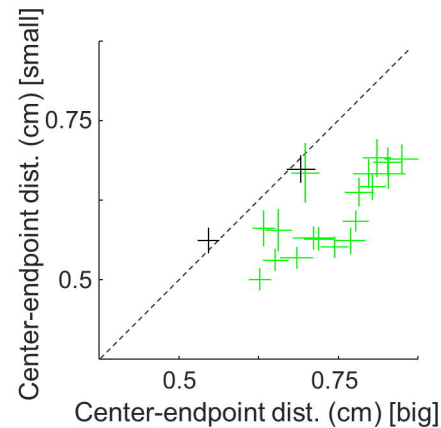
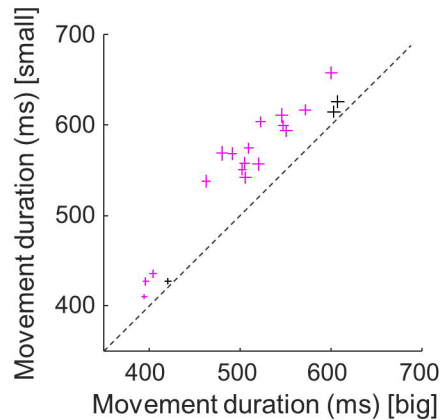
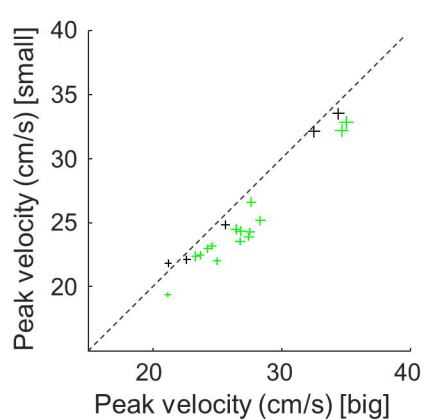
**A****Subject S6**

— Small-short block    ····· Small-long block    — Big-short block    ····· Big-long block

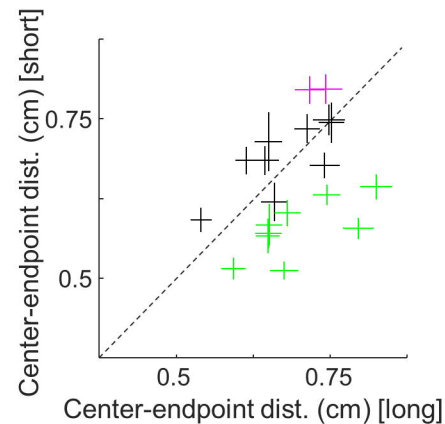
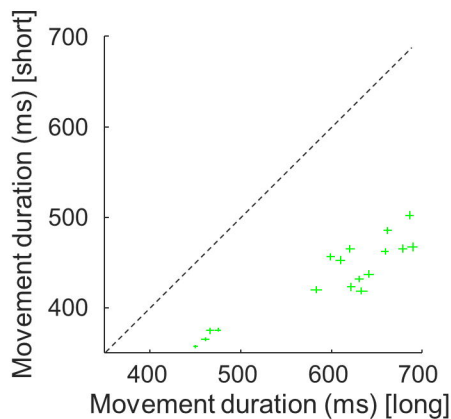
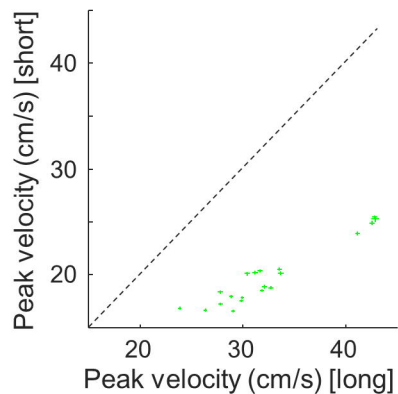
**B****Subject S6**

# Tokens task

## A Size contrast

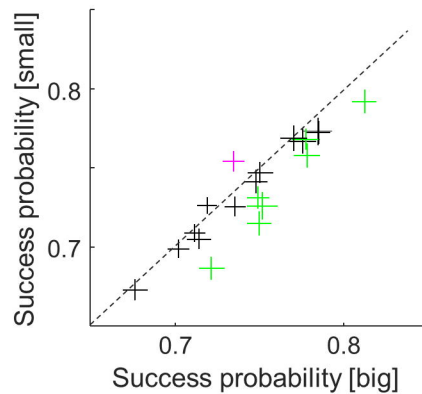
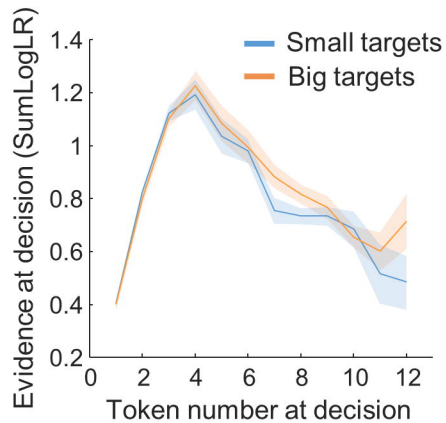
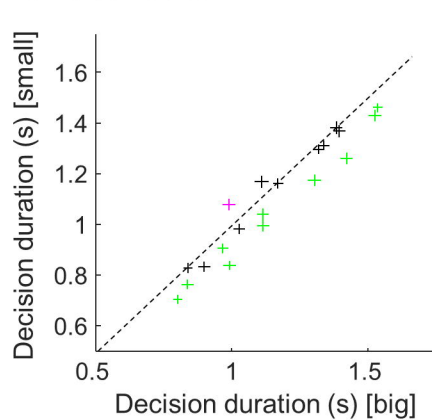


## B Distance contrast

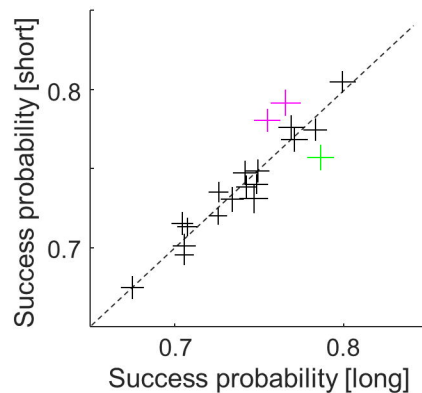
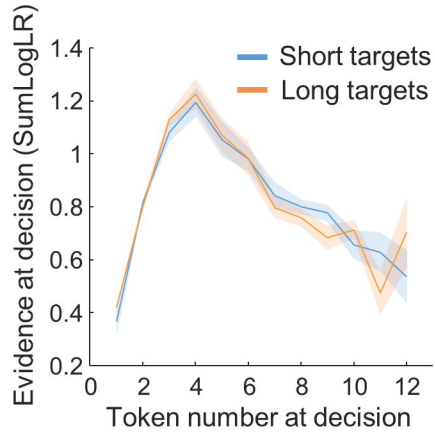
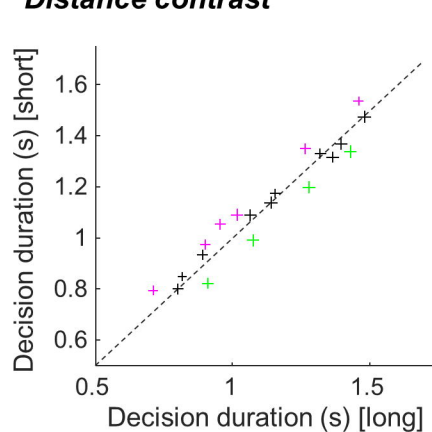


## Tokens task

### A Size contrast

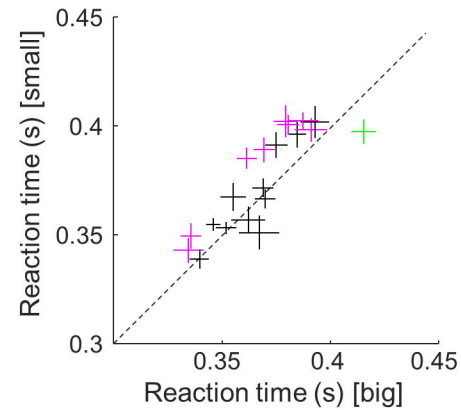


### B Distance contrast

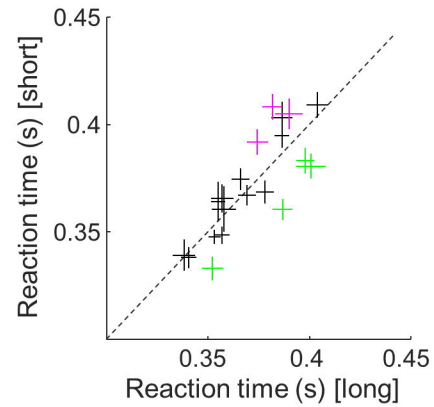


## DR task

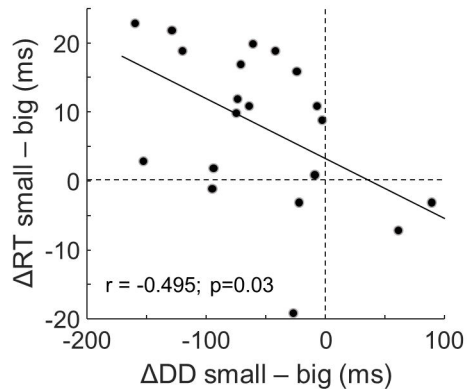
### C Size contrast



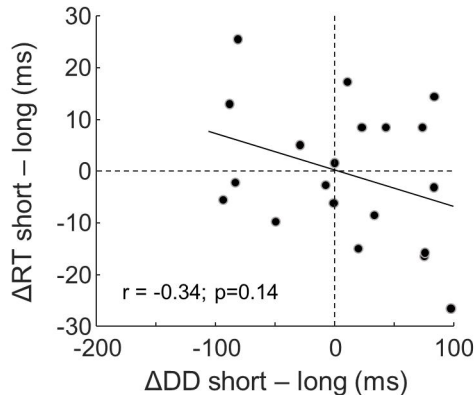
### D Distance contrast

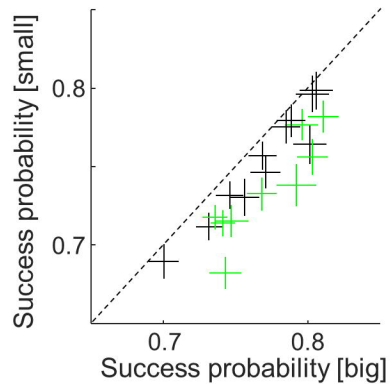
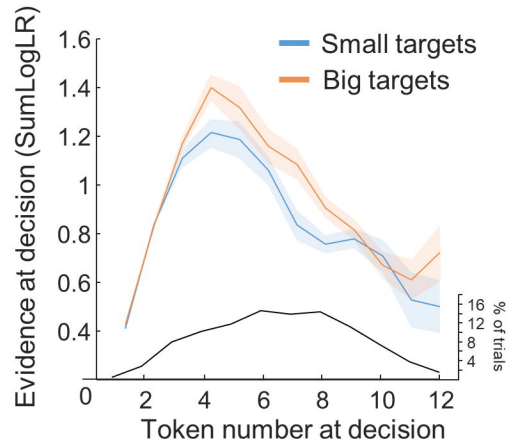
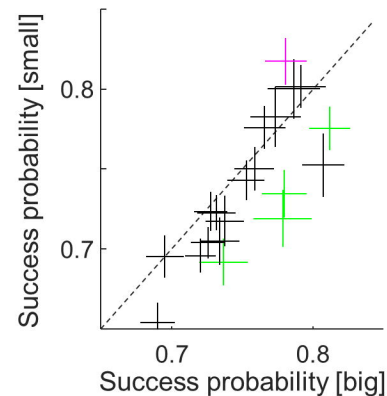
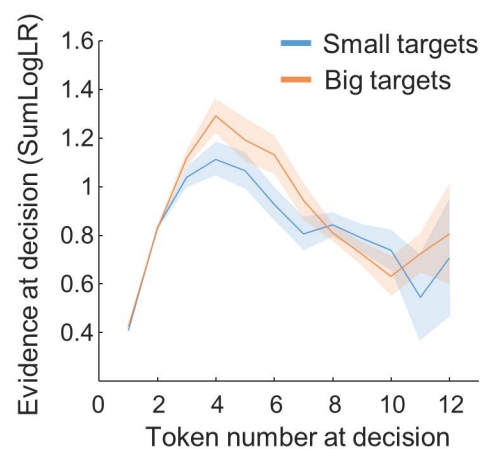
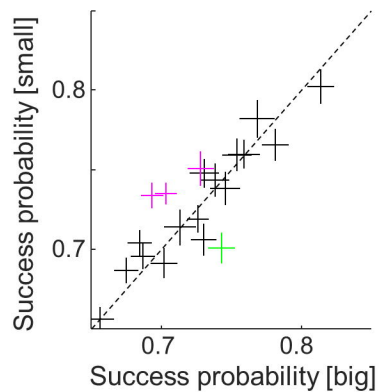
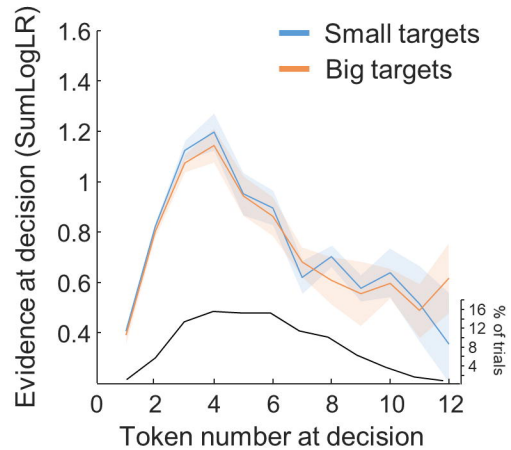
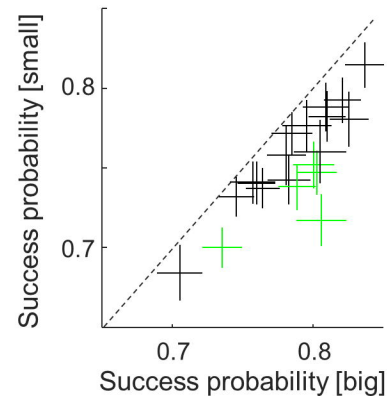
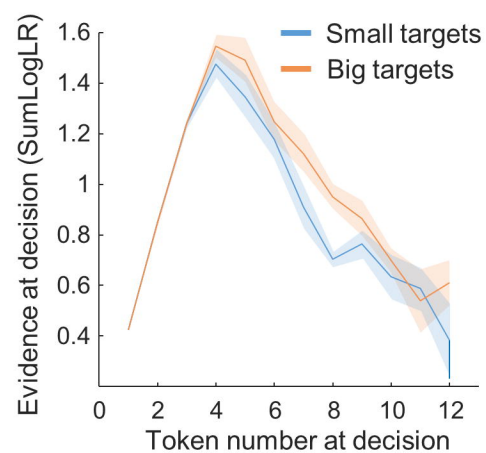


### Size contrast



### Distance contrast



**A Slow block****C Session #1****B Fast block****D Session #2**



*Slow block*

*Fast block*

