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

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ABSTRACT

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

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KEYWORDS

54   INTRODUCTION

55   Animals, including humans, are faced with decisions about actions on a daily basis, and they

56   behave in order to seek rewards while avoiding punishments and minimizing energy expenditure.

57   Because evaluation of reward, risk and effort governs our action choices, investigating how the

58   brain process these variables is critical to improve our understanding of adapted or dysfunctional

59   goal-directed behavior.

60   Importantly, the subjective value of a given activity is not only limited to its related reward, risks

61   and efforts. It also depends on the amount of time invested in it, as time strongly discounts the

62   value of rewards (Myerson and Green, 1995). Therefore, what is ultimately most adaptive is to

63   choose options that maximize one's global reward rate (Bogacz et al., 2010; Balci et al., 2011),

64   which occurs when the decision and action processes are sufficiently accurate but not overly

65   effortful and time consuming. As a consequence, nearly all decision scenarios present decision-

66   makers with speed-accuracy-effort trade-offs during both decision-making and action execution,

67   and the brain must control both processes to maximize the rate of reward.

68   Because trade-offs during decision and action have been typically studied in isolation, mechanisms

69   allowing a coordinated maximization of reward rate are still elusive. Recent promising advances

70   suggest, however, that motor control and choices, including economic ones, are governed by partly

71   overlapping optimization principles (Shadmehr et al., 2010, 2019; Haith et al., 2012; Choi et al.,

72   2014; Yoon et al., 2018; Carland et al., 2019). First, human and non-human primates move faster

73   and with a shorter reaction time toward items that they value more (Kawagoe et al., 1998;

74   Summerside et al., 2018; Revol et al., 2019). Second, humans take motor costs into account during

75   both motor (Cos et al., 2011, 2012, 2014; Morel et al., 2017) and perceptual (Burk et al., 2014;

76   Marcos et al., 2015; Hagura et al., 2017) decisions and effortful reaches impose a cost for decision-

77   making similar to cost functions in motor control (Wickler et al., 2000; Shadmehr et al., 2016;

78   Morel et al., 2017; Reppert et al., 2018). Finally, in the foraging paradigm where animals make

79   decisions regarding how long to stay and accumulate reward from one patch, and then move with

80   certain speed to another patch, the goods collection duration and the vigor (movement speed and

81   duration) with which human subjects move from one reward site to another are governed by a

82   mechanism allowing to maximize the overall capture rate (Yoon et al., 2018).

83   In line with this shared optimization hypothesis, we and others have proposed that control of

84   urgency is critical for reward rate maximization during decision-making between actions

85   (Ditterich, 2006; Churchland et al., 2008; Standage et al., 2011; Thura et al., 2012; Malhotra et al.,

86   2017, 2018). Urgency is a context-dependent, motor-related signal that grows over the time course

87   of a deliberation, pushing the decision-related neural activity toward the commitment threshold

88   (Thura and Cisek, 2014; Kira et al., 2015; Murphy et al., 2016; Steinemann et al., 2018).

89   Remarkably, we demonstrated in a changing evidence decision task that urgency level at decision

90   time strongly influences speed and duration of the following motor commands: early decisions,

91   usually made on the basis of strong sensory evidence but low urgency, were followed by long

92   movements (in terms of duration) whereas late decisions, relying on weak sensory evidence but

93   strong urgency, were followed by faster movements. Then, when subjects were encouraged to make

94   faster and less accurate decisions in distinct blocks of trials, movements were faster compared to

95   blocks encouraging slow and accurate choices. These results imply that a shared invigoration

96   signal, possibly computed in the basal ganglia, coordinates the unified adaptation of the speed-

97   accuracy trade-off during both decision-making and action execution in order to control the rate of

98   reward (Thura et al., 2014; Thura and Cisek, 2016, 2017; Cisek and Thura, 2018; Thura, 2020).

99   We proposed a model of this hypothetical mechanism, labelled the "shared regulation" hypothesis

100   (Figure 1A, Thura et al., 2014). In this model, speed-accuracy trade-offs for deciding and acting

101   are influenced by a shared decision urgency/movement vigor signal. As a consequence, the context-

102   dependent urgency level at which a decision is made should determine the vigor (duration and

103   speed scaled by amplitude) of movements produced to express this choice and conversely, the

104   context-dependent vigor of movements executed to express a choice should predict the level of

105   urgency with which that choice is made. Recent behavioral and neurophysiological data collected

106   in both trained monkeys and naïve humans strongly support the former prediction (Thura et al.,

107   2014; Thura and Cisek, 2016; Thura, 2020). The latter prediction, namely whether or not the fastest

108   choices are made in motor contexts encouraging the most vigorous movements (Figure 1B),

109   remains, however, to be tested.

110   To this aim, we conducted an experiment in which human subjects performed a probabilistic

111   decision task in which perceptual choices were expressed by reaching movements toward targets

112   whose size and distance from the starting point varied across blocks of trials, allowing us to assess

113   the effects of the motor context on subjects' decision policy.
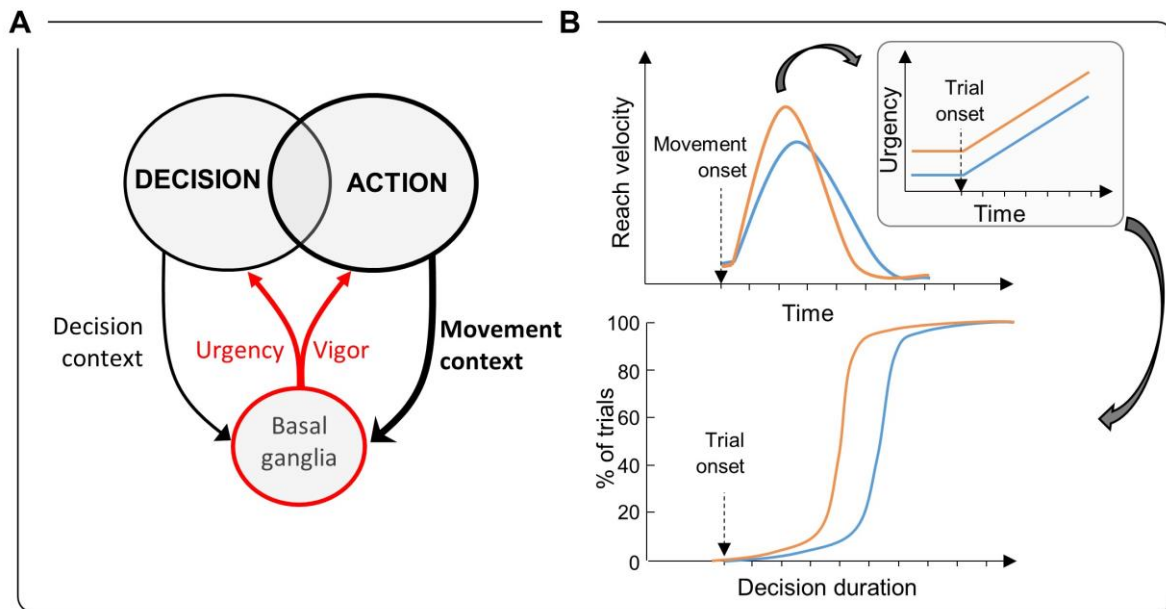
Figure 1: The "shared regulation" hypothesis. A. Simplified hypothetical mechanism of a shared regulation of decision and movement durations by one unique invigoration (decision urgency/movement vigor) signal, possibly computed in the basal ganglia (Thura et al., 2014; Thura and Cisek, 2017). The thick black lines illustrate the manipulation of the motor context, tested in the present study, leading to the modulation of the urgency/vigor signal. B. The shared regulation hypothesis makes a simple prediction regarding the effect of the motor context in which a decision is made on the duration of that decision: if a context encourages execution of vigorous (faster, shorter) movements (orange) to report choices, then the urgency level in this context should be raised compared to another context in which movements need to be less vigorous but more accurate (blue). As a consequence, equally difficult decisions made in the vigorous block of trials should be on average shorter than those made in the block encouraging slow and accurate movements.

MATERIALS AND METHODS

Participants

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

136 *Dataset*

137 The decision and motor behaviors of most of subjects (17/20) have been described in a recent

138 publication whose aim was to report the effect of decision strategy on movement properties in

139 human subjects (Thura, 2020). This analysis showed that according to the shared regulation

140 hypothesis, the urgency level at time of decision commitment strongly influences movement

141 kinematics, with urgency-based decisions leading to vigorous movements. In the present paper,

142 we analyzed data of the same subjects along with data from 3 additional ones, but we grouped trials

143 depending on movement constraints (target size/movement amplitude configurations, see below),

144 allowing us to test on the same subjects the reverse side of the shared regulation hypothesis, i.e.

145 the effects of motor context on decision policy.

146 *Setup*

147 The subjects sat in an armchair made planar reaching movements using a lever held in their

148 dominant hand. A digitizing tablet (GTCO CalComp) continuously recorded the lever horizontal

149 and vertical positions (100 Hz with 0.013cm accuracy). Target stimuli and cursor feedback were

150 projected by a DELL P2219H LCD monitor (60 Hz refresh rate) onto a half-silvered mirror

151 suspended 26 cm above and parallel to the digitizer plane, creating the illusion that targets floated

152 on the plane of the tablet. Unconstrained eye movements and pupil area of a subset of subjects were

153 recorded using an infrared camera (ISCAN, sampling rate of 120 Hz, data not shown).

154 *Tasks*

155 The subjects performed a modified version of the tokens task (Figure 2A, see Cisek et al., 2009 for

156 the original version). They were faced with a visual display consisting of three blue circles (1.5 cm

157 radius) placed horizontally at a distance of 6 cm of each other (the "decision" stimuli). In the central

158 blue circle 15 small tokens were randomly arranged. Positioned 12 cm below, three black circles,

159 organized horizontally as well defined the "movement" stimuli. While the central black circle

160 radius was kept constant at 0.75 cm, the size of the two lateral black circles and their distance from

161 the central circle could vary, set to either 0.75 (small) or 1.5 cm (big) of radius, and to either 6

162 (short) or 12 cm (long) of distance from the central circle, in distinct blocks of trials. This design

163 allowed us to define four motor blocks depending on the size/distance combination of the two

164 targets: "small/short", "small/long", "big/short" and "big/long" (Figure 2B).

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Impact of a demanding movement on decision-making
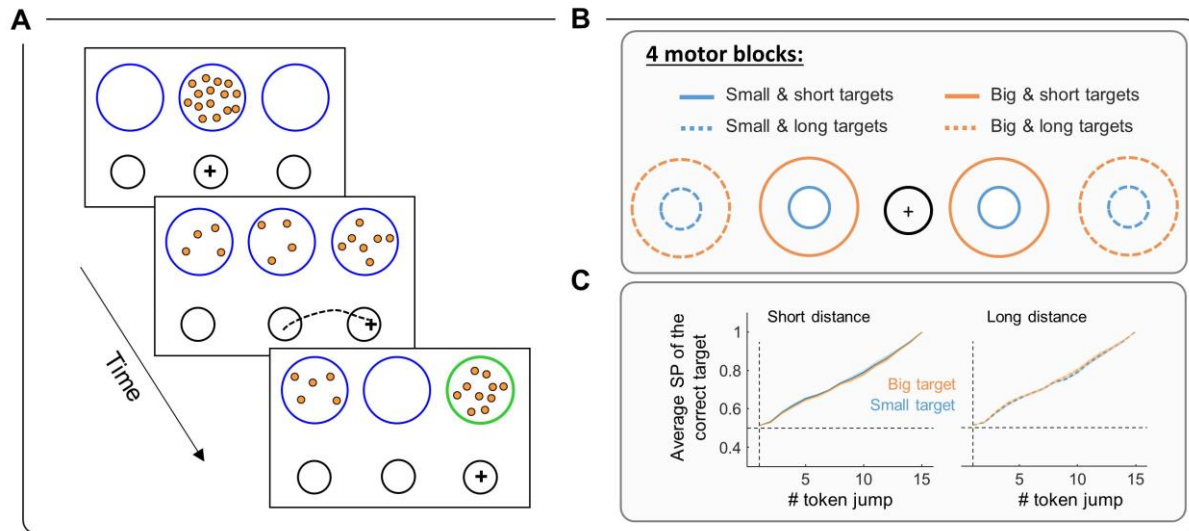
Figure 2: Experimental design and conditions. A. Time course of a trial in the tokens task. B. Motor conditions, i.e. movement target size and distance combinations. In distinct blocks of trials, both lateral targets could be either small and located close to the starting circle (black), small and located far from the starting circle, big and located close to the starting circle or big and located far from the starting circle. C. Average success probability profiles of trials experienced by subjects in each of the four motor conditions.

A trial was initiated when the subject moved and hold the lever into the small black central circle (starting position) for 500ms. Tokens then started to jump, one by one, every 200ms in one of the two possible lateral blue circles. The subjects' task was to decide which of the two lateral blue circles would receive the majority of the tokens at the end of the trial. They reported their decisions by moving the lever into the lateral black circle corresponding to the side of the chosen blue circle. Importantly, subjects were allowed to make and report their choice at any time between the first and the last jump. Arm movement duration could not exceed 800ms, irrespective of the motor block. If a movement exceeds 800ms (too slow) or if it reaches the target but fails to stop in it within 800ms (inaccurate), the trial is considered as a movement error trial. Once the choice is properly reported, the remaining tokens jumped more quickly to their final circles. In separate blocks of trials, this post-decision interval was set to either 20ms ("fast" decision block) or to 150ms ("slow" decision block). The acceleration of the remaining tokens implicitly encouraged subjects to decide before all tokens had jumped into their respective lateral circles, to save time and increase their rate of reward. Note that each reaching movement carries a temporal cost with respect to reward rate maximization (see equation 3) because the remaining tokens accelerate only

188   when action is completed. After holding the lever in the target for 500ms, a visual feedback about

189   decision success or failure (the chosen decision circle turning either green or red, respectively) was

190   provided after the last token jump. A 1500ms period (the inter-trial interval) preceded the following

191   trial.

192   Before and after the tokens task described above, each subject also performed 100 trials of a

193   delayed reach task (DR task). This task was identical to the tokens task except that there was only

194   one lateral decision circle displayed at the beginning of the trial (either at the right or at the left

195   side of the central circle with 50% probability) and all tokens moved from the central circle to this

196   unique circle at a GO signal occurring after a variable delay (1000 ± 150ms). They executed 2

197   different motor blocks of 25 trials each before the tokens task and the 2 other motor blocks (25

198   trials each) after the tokens task. This DR task was used to estimate the sum of the delays

199   attributable to sensory processing of the stimulus display as well as to response initiation in each

200   motor condition.

201   *Instructions*

202   In a given session, subjects were asked to complete one slow decision block and one fast decision

203   block of the tokens task. To complete a decision block (either fast or slow), subjects had to make

204   160 correct choices, indirectly motivating them to optimize successes per unit of time. After the

205   first block was completed, a short break was offered to the subject. Within each decision block, the

206   size of the movement targets and their distance from the starting circle, i.e. the motor blocks, were

207   varied every 40 trials. In a session, each motor block was thus performed twice, once in the slow

208   decision block, and once in the fast decision block.

209   Subjects performed two sessions (test-retest design), one a day and each of them separated by a

210   maximum of 7 days. In session #1 subjects always started the tokens task in the slow decision block

211   with the following succession of motor blocks: small/short, small/long, big/short and big/long;

212   followed by the execution of the fast decision block with the same motor blocks order. To prevent

213   any block-related confounding effect, the order of decision and motor blocks presentation was

214   reversed in session #2. Before the first session, we explicitly described to the subjects the principle

215   of each decision block, specifying that deciding quickly in the fast block was more advantageous

216   in terms of time saving than in the slow block (because of the larger acceleration of the remaining

217   tokens) but that such hasty behavior could also lead to more erroneous decisions. A short recall

218   was provided before starting the second session. Because subjects were informed that they had to

219   complete a given number of correct responses in each session, they were all aware that they were

220   presented with a speed/accuracy trade-off in this task. A practice period consisting of performing

221   20 tokens task trials in the slow decision and big/short motor blocks was proposed at the beginning

222   of the first session, mainly allowing subjects to get familiar and comfortable with the manipulation

223   of the lever on the tablet. Among the 23 subjects who participated in this study, two have been

224   tested six and seven times. The additional sessions performed by these two subjects are not

225   described in the present report.

226   *Data analysis*

227   All arm movement data were analyzed off-line using MATLAB (MathWorks). Reaching

228   characteristics were assessed using subjects' movement kinematics. Horizontal and vertical

229   position data were first filtered using a tenth degree polynomial filter and then differentiated to

230   obtain a velocity profile. Onset and offset of movements were determined using a 3.75 cm/s

231   velocity threshold. Peak velocity was determined as the maximum value between these two events

232   and endpoint error was defined as the Euclidian distance separating the target center from the

233   movement endpoint location. Dispersion of movement end points is visualized with confidence

234   ellipses representing an iso-contour of the Gaussian distribution, defining the region that contains

235   95% of all samples in each condition.

236   We computed at each moment during a trial the success probability $p_i(t)$ associated with choosing

237   each target i. For a total of 15 tokens, if at a particular moment in time the right target contains N_R

238   tokens, whereas the left contains N_L tokens, and there are N_C tokens remaining in the center, then

239   the probability that the target on the right will ultimately be the correct one (i.e., the success

240   probability of guessing right) is as follows:

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

241   To characterize the success probability profile of each trial, we calculated this quantity (with

242   respect to either the correct target or the target ultimately chosen by the subject, depending on

243   purposes) for each token jump. To ensure that difficulty of decisions was homogeneous among

244   subjects and experimental conditions, we controlled the sequence of trials experienced by subjects

245   in each session. Especially, we interspersed among fully random trials (20% of the trials in which

246   each token is 50% likely to jump into the right or the left lateral circle) three special types of trials

247   characterized by particular temporal profiles of success probability. Subjects were not told about

248   the existence of these trials. 30 % of trials were so-called "easy" trials, in which tokens tended to

249   move consistently toward one of the circles, quickly driving the success probability $p_i(t)$ for each

250   toward either 0 or 1. Another 30% of trials were "ambiguous", in which the initial token movements

251   were balanced, making the $p_i(t)$ function close to 0.5 until later in the trial. The last special trial

252   type was called "misleading" trials (20%) in which the 2-3 first tokens jumped into the incorrect

253   circle and the remaining ones into the correct circle. In all cases, even when the temporal profile of

254   success probability of a trial was predesigned, the actual correct target was randomly selected on

255   each trial. Importantly, the sequence of trials was designed such as proportion of each trial type

256   was similar in each decision and motor condition (Figure 2C).

257   To estimate the time at which subjects committed to their choice (decision time, DT) on each trial

258   in the tokens task, we detected the time of movement onset, defining the subject's reaction time

259   (RT) and subtracted from it her/his mean sensory-motor delays (SM) estimated based on her/his

260   reaction times in the same motor block of the delayed reach task performed the same day. Decision

261   duration (DD) was computed as the duration between DT and the first token jump. Equation 1 was

262   then used to compute for each trial the success probability at the time of the decision (SP).

263   Calculation of subjects' accuracy criterion at decision time relies on the available sensory evidence

264   at that time. Because it is very unlikely that subjects can calculate Equation 1, we computed a

265   simple "first order" approximation of sensory evidence as the sum of log-likelihood ratios

266   (SumLogLR) of individual token movements as follows (Cisek et al., 2009, page 11567, provides

267   more details on this analysis):

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

268   where $p(e_k|S)$ is the likelihood of a token event e_k (a token jumping into either the selected or

269   unselected target) during trials in which the selected target S is correct, and $p(e_k|U)$ is its likelihood

270   during trials in which the unselected target U is correct. The SumLogLR metric is thus proportional

271   to the difference in the number of tokens which have moved in each circle before the moment of

272   decision. To characterize the decision policy of a given subject in a given block of trials, we binned

273   trials as a function of the total number of tokens that moved before the decision, and calculated the

274   average SumLogLR for each bin.

275   To quantify subjects' performance relative to the task objective, i.e. complete a given number of

276   correct decisions, assuming they tried to compete each block as quickly as possible, we first

277   calculated for correct and bad decisions the reward rate (RR), using a local definition (Haith et al.,

278   2012; Thura et al., 2012) which corresponds to the expected number of correct choices per unit of

279   time. This is computed as follows:

$$RR_n = \frac{SP_n}{DD_n + SM + MD_n + RD_n + ITI} \tag{3}$$

280   where SP_n is the probability that the choice made on trial n was correct, DD_n is the time taken to

281   make the decision, SM is the sensori-motor delays (specific to each motor context but constant for

282   a given session), MD_n is the movement duration, RD_n is the duration of the remaining token jumps

283   after the target is reached, and ITI is the inter-trial interval (fixed at 1500ms). Then from the average

284   reward rate computed in each motor block we calculated the average number of correct choices per

285   minute and deducted from it the time necessary to complete a given number of correct choices in

286   each condition of interest.

287   Comparisons of decision duration, success probability, movement duration, peak velocity,

288   accuracy and block duration between conditions performed for each subject are statistically tested

289   with Wilcoxon-Mann-Whitney (WMW, two-sided rank-sum) tests. The effect of motor condition

290   on sensory evidence at decision time as a function of decision duration is statistically tested with

291   analyses of covariance (ANCOVAs). For these analyses, very fast decisions made before token

292   jump #4 are discarded. Decisions made before jump #4 were rare (see Thura, 2020) and success

293   probability homogeneity (if subjects decide before token jump #4 it is likely because the first three

294   tokens jumped into the same target) at that time makes data exclusion reasonable. Proportions of

295   inadequate movements in small target conditions (small/short and small/long blocks) is statistically

296   compared to proportion of inadequate movements in big target conditions (big/short and big/long

297   blocks) for each subject with chi-square tests. For all statistical tests, the significance level is set a

298   0.05.

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302   RESULTS

303   *Effect of motor context on motor behavior in the tokens task*

304   As expected, the motor context in which decisions were reported strongly influenced subjects'

305   movement properties and performance. First, we calculated the percentage of trials in which an

306   inadequate movement was performed to express a choice, i.e. a movement exceeding 800ms (too

307   slow) or failing to stop and maintain position in the target within 800ms (inaccurate). In the first

308   session, most subjects (18/20) performed significantly more inadequate movements in the

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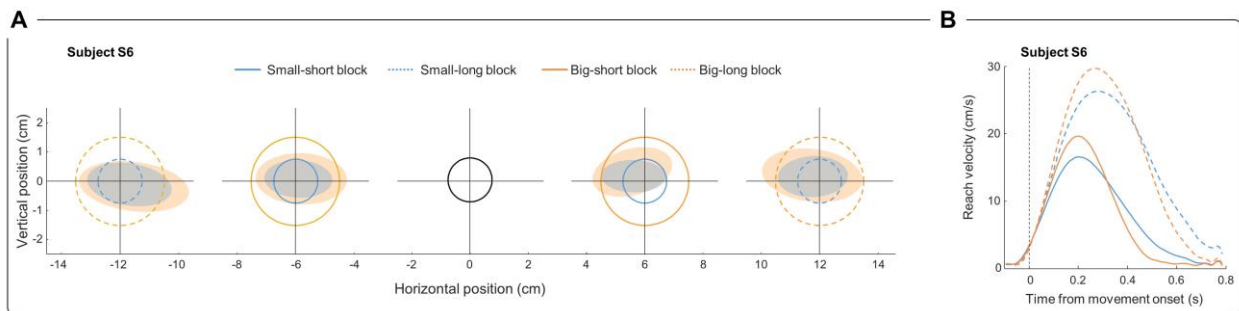
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311   ***Figure 3: Motor behavior in one example subject.*** *A. Panel shows the motor visual display*
312   *depicted in Figure 2, along with shaded ellipses illustrating for each motor condition and side*
313   *with respect to the start circle (black) the dispersion (an iso-contour of the Gaussian*
314   *distribution) of one example subject reaching endpoints in the tokens task. Each ellipse*
315   *contains 95% of the data in each condition, and trials include correct and inadequate (too*
316   *slow or inaccurate) movements executed in the two sessions and in the two decision conditions*
317   *(slow and fast). B. Reach velocity profiles of the same subject in the four motor conditions.*
318   *Same color/style convention as in A. Only adequate movements are included.*

319

320   small target (small/short and small/long blocks) condition compared to the big target (big/short and

321   big/long blocks) condition (Chi-square tests, p < 0.05). Movement "error" rates within blocks are

322   the following across the population: small/long target blocks:18.8% ± 6.8; small/short: 5.5% ±3.1;

323   big/long: 4.5% ± 2.7; big/short: 1% ±1.3. Despite an overall slight decrease, the same impact of

324   motor constraint was observed on movement error rate during session #2: 19 out of 20 subjects

325   made more inadequate movements in the small target compared to the big target condition (Chi-

326   square tests, p < 0.05), with the following error rates in each of the four motor contexts: small/long

327   target blocks: 16.7% ±4.5; small/short: 4.8% ±1.8; big/long: 2.35% ±1.5; big/short: 1.1% ±1.3).

328   Figure 3A shows the dispersion of movement endpoints in one example subject who performed the

329   tokens task in the four motor blocks. In this plot, correct and inadequate (too slow or inaccurate)

330   movements trials are included. Confidence ellipses (containing 95% of all samples in each

331   condition) largely extend outside of movement targets in small target trials, especially when targets

332   are far from the starting center, whereas they almost entirely fit into movement targets in big target

333   trials.

334   Then, we focused analyses on trials in which an adequate movement was performed to express a

335   choice, irrespective of the outcome of that choice. As expected, reaching movement properties, in

336   terms of velocity peak, duration and endpoint "error" (the distance between target center and

337   movement offset location) were affected by the motor context in which movements were executed.

338   Figure 3B shows for the same representative subject the reaching velocity profiles in trials sorted

339   as a function of the four motor blocks. Unsurprisingly, movement velocity was largely higher and

340   duration longer in long target (dotted lines) compared to short target trials (solid lines), regardless

341   of the size of the target. The size of the target also modulated movement speed and duration but to

342   a lesser extent. Movements were indeed slightly faster and shorter when executed toward big

343   targets (orange lines) compared to those executed toward small targets (blue lines).

344   This effect of motor context on movement properties was observed on the vast majority of subjects

345   performing either the tokens or the delayed reach (DR) task. To simplify comparisons in the

346   following analyses, we grouped trials depending on (1) target size, defining two conditions, small

347   versus big target conditions, regardless of target distance from the starting circle, and (2) target

348   distance from the starting circle, defining two other conditions, short versus long target conditions,

349   regardless of target size.

350   First, most of subjects reported decisions by making significantly faster (15 out of 20 subjects,

351   WMW test, $p < 0.05$), shorter, in terms of duration (17 out of 20 subjects, WMW test, $p < 0.05$) and

352   more dispersed (18/20, WMW test, $p < 0.05$) movements in the big target compared to the small

353   target condition (figure 4A). Second, all subjects reached long targets with significantly faster and

354   longer movements compared to movements executed toward short targets (WMW test, $p < 0.05$,

355   figure 4B, left and middle panels). In this distance contrast, we observed that endpoint distances

356   from target center were not as consistently modulated as in the size contrast, being significantly

357   larger for the long target compared to the short target condition in only 9 out of 20 subjects (WMW

358   test, $p < 0.05$, figure 4B, right panel). The same influence of target characteristics on reaching

359   velocity, duration and accuracy was found in the DR task (not shown). Finally, the influence of

360   target characteristics on movement parameters was similar in the two experimental sessions and in

361   the two decision blocks (slow and fast, not shown).

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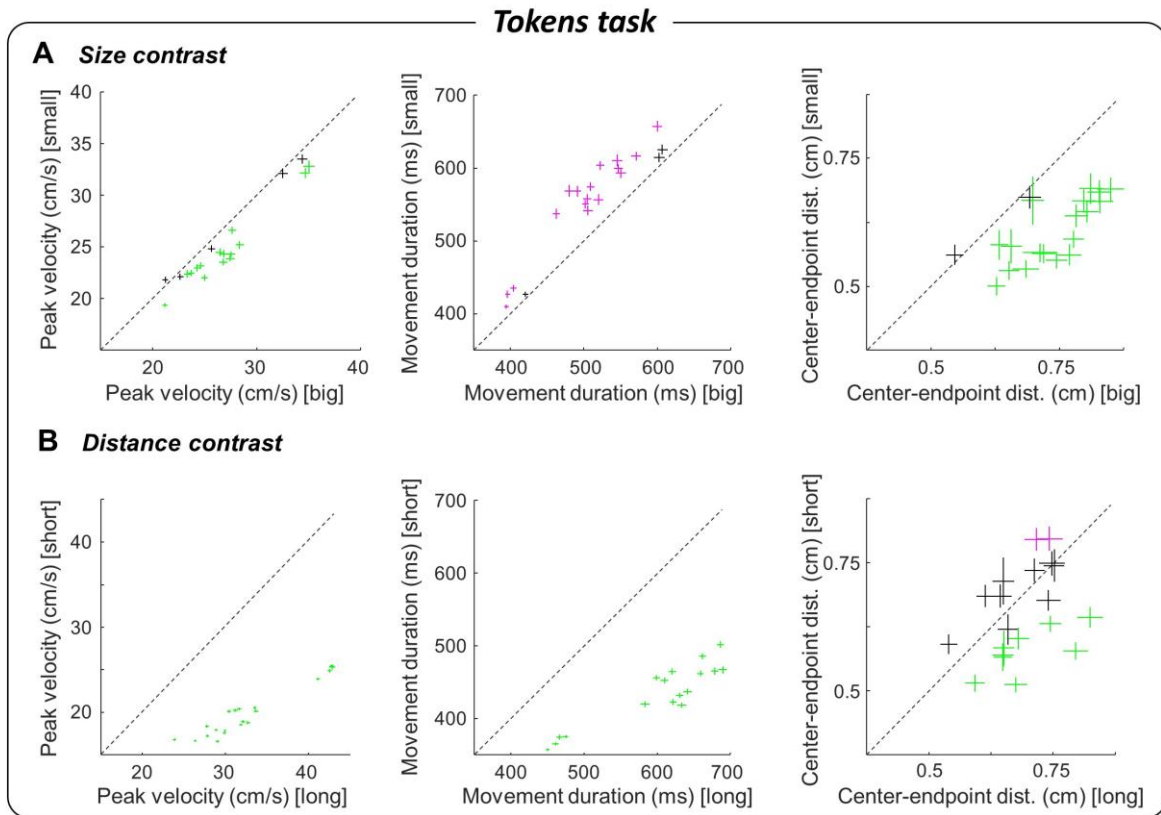
Figure 4: Effect of motor context on population motor behavior. *A. Average reaching movement peak velocity (left), duration (middle) and target center-endpoint distance (right) of each subject during big target (big/short and big/long blocks, x-axis) and small target (small/short and small/long blocks,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

374   To summarize, manipulating the target characteristics in distinct blocks of trials successfully

375   modulated reaching movement properties, encouraging subjects to either emphasize speed or

376   accuracy to execute movements in these blocks to express their choices. In the following section,

377   we assess whether or not these context-dependent adjustments of motor parameters influenced the

378   decision policy leading to the actions executed to report choices.

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379   *Effect of motor context on subjects' decision behavior*

380   To determine the potential impact of movement context on decision policy, we first analyzed

381   subjects' decision duration (regardless of the decision outcome) by sorting trials depending on

382   target characteristics, irrespective of the session and the decision condition (slow or fast).

383   By first comparing decisions made in big (big/short and big/long) versus small (small/short and

384   small/long) target trials, we found that decisions were overall shorter in the small target compared

385   to the big target condition (1099 versus 1154ms). Importantly, difference is significant for half of

386   the population (WMW test, p<0.05, figure 5A, left panel). Only one subject behaved the opposite

387   way, making significantly faster choices when allowed to report them with fast, less accurate

388   reaching movements. Importantly, we found virtually no difference between the average decision

389   difficulties (quantified as success probability profiles, see Methods and figure 2C) in the two motor

390   conditions, excluding a role of the sensory evidence experienced by the subjects in the difference

391   of decision duration observed between small and big target contexts. Did this shortening of decision

392   duration affect choice accuracy? To answer that question, we analyzed the amount of sensory

393   evidence that subjects needed to commit to their choices (i.e. their accuracy criterion, computed as

394   the sum of the log-likelihood ratios, see Methods), as a function of decision duration for the two

395   motor conditions, small and big target trials (Figure 5A, middle panel). First, the level of sensory

396   evidence that subjects required before committing to a choice decreased as a function of decision

397   duration, irrespective of motor conditions (ANCOVA, SumLogLR, time effect, $F_{(1,347)} = 164$, p <

398   0.0001). This observation suggests that the more time is elapsing over the time course of a trial,

399   the more decisions rely on a sensory-agnostic signal. In our previous studies as well as in others,

400   this decreasing accuracy criterion is interpreted as a behavioral signature of an urgency-gating

401   mechanism of decision-making, which in short describes the decision variable as the combination

402   of sensory evidence with an urgency signal and the decision is made when the decision variable

403   reaches a constant threshold (Cisek et al., 2009; Thura et al., 2012).

404   Importantly for the present report, we found that the accuracy criterion of subjects performing the

405   tokens task in small target trials was significantly lower than in big target trials, for any decision

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

407   indicates that subjects were more willing to tolerate less sensory evidence to make their choices in

408   small target compared to big target trials. As a consequence, decisions were usually less likely to

409   be correct in the small target compared to the big target context (Figure 5A, right panel). This

15

410   decrease of success probability in small target trials was significant in 7 out 10 subjects showing a

411   significant decrease of decision duration as a function of target size (WMW test, p<0.05).

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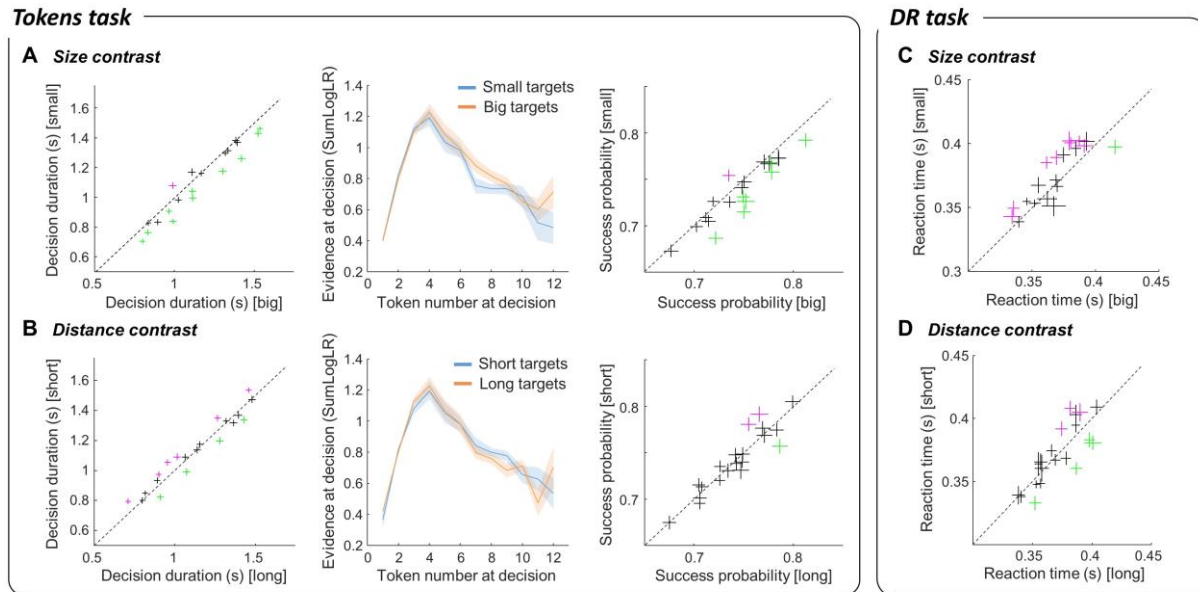
413

414   ***Figure 5 : Effect of motor context on decision behavior***. *A. Left: Average decision duration*
415   *of each subject during big (x-axis) and small (y-axis) target conditions performed in the tokens*
416   *task. Same convention as in Figure 4. Middle: Average (± SE) evidence at decision time across*
417   *subjects as a function of decision duration in the small (blue) and the big (orange) target*
418   *conditions of the tokens task. Right: Mean success probability of each subject during big (x-*
419   *axis) and small (y-axis) target conditions performed in the tokens task. Same convention as in*
420   *Figure 4. Data include trials collected from both sessions #1 and #2, in both the slow and fast*
421   *decision blocks. B. Same as A for trials executed in the long versus short target conditions. C.*
422   *Average reaction time of each subject during big (x-axis) and small (y-axis) target conditions*
423   *performed in the delayed reach task. D. Same as C for trials executed in the long (x-axis)*
424   *versus the short (y-axis) target condition.*

425

426   We next compared decision durations in short versus long target trials, a contrast that strongly

427   modulates movement speed of all subjects (Figure 4B, left panel). We found that the impact of

428   target distance, and thus movement speed, on decision duration was less consistent at the

429   population level compared to the impact of target size described above (Figure 5B, left panel).

430   Indeed, we observed that 6 subjects made significantly longer decisions in the short target

431   compared to the long target condition (WMW test, p<0.05), 4 subjects behaved the opposite way

432   (WMW test, p<0.05), and the 10 remaining ones did no behave differently, in terms of decision

433   duration, between the two motor conditions. We also found that target distance did not significantly

434 influence the quantity of sensory information used by subjects to commit to their choice

435 (ANCOVA, SumLogLR, target size effect, $F_{(1,346)} = 0.13$, $p = 0.72$, Figure 5B, middle panel), and

436 the success probability of these choices was only rarely significantly modulated as a function of

437 target distance (Figure 5B, right panel).

438 We next analyzed the effect of target size and distance on subjects' reaction times (RT) in the

439 delayed reach (DR) task. In the DR task, no volitional commitment needed to be made as subjects

440 were instructed with both the correct target and when to execute their response (see Methods). In

441 this task we found that subjects' RTs were overall longer in small target compared to big target

442 trials (375 versus 367ms), with a significant difference for 8 out of 20 subjects (WMW test,

443 p<0.05), and only one subject behaving significantly the opposite way (Figure 5C). Interestingly,

444 we found a significant correlation between the modulation of decision duration by target size in the

445 tokens task and the modulation of reaction time in the same conditions in the DR task. In other

446 words, the more subjects expedited decisions in the small target condition of the tokens tasks, the

447 more they slowed down their response initiation in the same condition in the DR task (Pearson

448 correlation, $r = -0.495$, $p = 0.026$, Figure 6). By contrast, reaction times were less homogeneously

449 affected by the distance condition in the DR task. Four subjects reacted faster in short compared to

450 long target blocks, and 3 subjects behaved the opposed way (WMW test, p<0.05, Figure 5D).
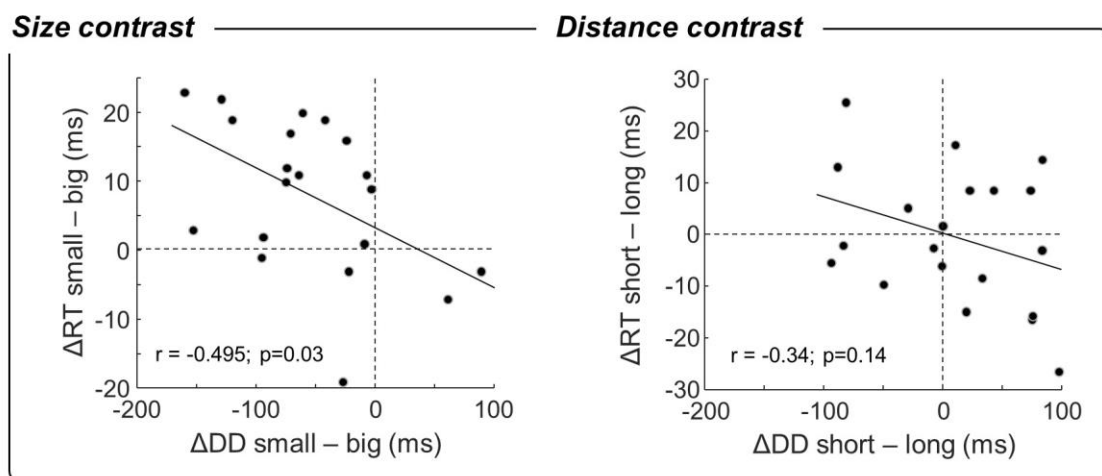
451

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

457   To assess whether the effect of target size on decision policy was dependent on the decision context,
458   i.e. the slow or fast decision blocks of the tokens task, we computed subjects' decision duration,
459   success probability and sensory evidence at decision time for each of the two size conditions,
460   separately for the two decision blocks. In a recent report (Thura, 2020), we describe in detail
461   subjects' behavior in the two decision conditions. Quickly, the "slow" decision block of trials
462   encourages slow and accurate decisions because the tokens that remain in the central decision circle
463   after movement completion accelerate only a little compared to the pre-decision period (see
464   Methods).
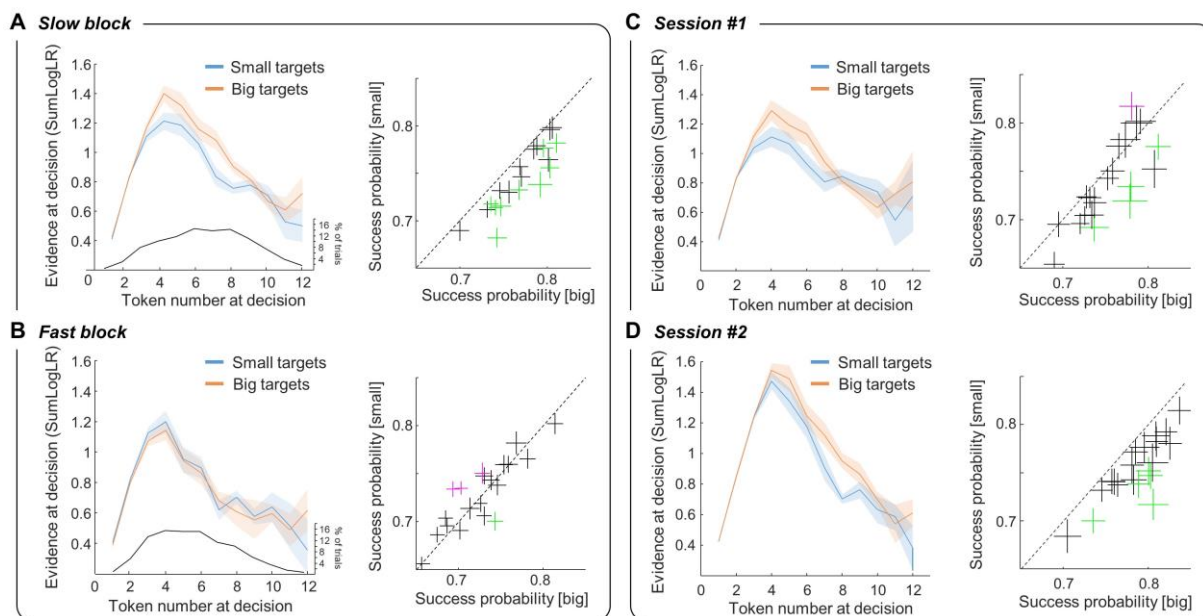
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466   *Figure 7: Effect of motor context on decision accuracy depending on decision context and*
467   *experience. A. Left: Average (± SE) evidence at decision time across subjects as a function of*
468   *decision duration in small (blue) and big (orange) target conditions performed in the "slow"*
469   *decision block of the tokens task. The black line below shows the average distribution of*
470   *decision duration across subjects in the slow block. Right: Average success probability of each*
471   *subject during big (x-axis) and small (y-axis) target conditions performed in the slow decision*
472   *block of the tokens task. Data from both sessions #1 and #2 are included. Same convention as*
473   *in Figure 4. B. Same as A for decisions made in the "fast" decision block of the tokens task.*
474   *C. Same as A for decisions made in the first session, including only slow decision blocks. D.*
475   *Same as C for decisions made during the second session.*

476

477   By contrast, in the "fast" block of trials, the remaining tokens accelerate a lot, allowing subjects to
478   potentially save a lot of time by deciding quickly, permitting to eventually maximize their reward
479   rate. In Thura, 2020 we showed that subjects behaved accordingly, making faster (1028 vs 1229ms

480　across subjects) and less accurate (0.87 versus 0.97) decisions in the fast block compared to the

481　slow block of trials (see the average distributions of decision duration across subjects in the two

482　decision blocks in Figure 7A,B). In the present report, we demonstrate that the impact of target size

483　on decision policy, especially accuracy, is larger in the slow block than in the fast block of trials.

484　Indeed, decision durations were significantly modulated by target size in 8 out of 20 subjects

485　performing the slow block whereas they were modulated in only 6 subjects performing the tokens

486　task in the fast condition (WMW test, p<0.05). Moreover, the accuracy criterion was significantly

487　higher for big target compared to small target trials in the slow block (ANCOVA, SumLogLR, size

488　effect, $F_{(1,345)} = 13.6$, p = 0.0003) but not in the fast block ($F_{(1,298)} = 0.1$, p = 0.75, Figure 7A,B, left

489　panels). As a consequence, success probability was strongly influenced by target size in the slow

490　block (significantly modulated in 9 out of 20 subjects, WMW test, p<0.05) whereas effects were

491　more balanced in the fast blocks (Figure 7A,B, right panels).

492　Next, we analyzed the effect of target size on decision policy depending on the level of experience

493　of subjects in the tokens task. To do this, we computed subjects' decision duration, success

494　probability and sensory evidence at decision time for decisions made in the slow decision block for

495　each of the two target size conditions, separately for the two experimental sessions. Overall, we

496　found that the impact of target size on decision policy did not strongly evolve with training.

497　Decision durations were slightly more modulated by target size in the first session than in the

498　second sessions (5/20 and 3/20 subjects with a significant effect of target size on decision duration

499　in session #1 and #2, respectively; WMW test, p<0.05), but accuracy criterion (ANCOVA,

500　SumLogLR, size effect, $F_{(1,320)} = 2.5$, p=0.1 in session #1; $F_{(1,330)} = 10.5$, p=0.0013 in session #2)

501　and to a lesser extent, success probability (4/20 and 5/20 subjects with a significant effect of target

502　size on decision duration in session #1 and #2, respectively; WMW test, p<0.05) were more

503　affected by target size in session #2 compared to session #1 (Figure 7C,D).

504

Impact of a demanding movement on decision-making
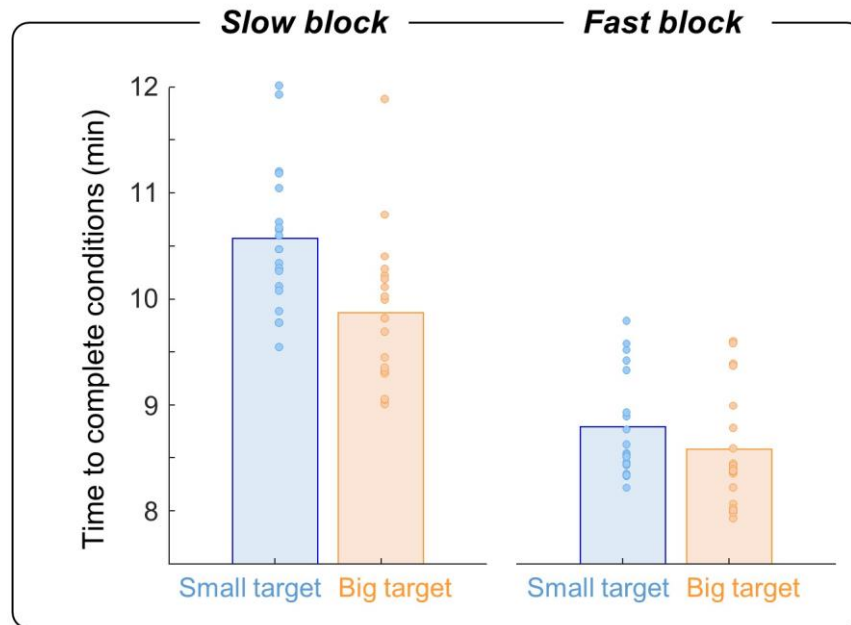
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506 ***Figure 8: Influence of target size on the expected duration of blocks.*** *Bars show the average*
507 *expected time necessary to complete a block of 80 trials, computed based on reward rate in*
508 *each condition, in the small (blue) and big (orange) target block across subjects and sessions,*
509 *in the slow (left) and fast (right) decision block of trials. Dots illustrate individual data.*

510

511 Finally, we evaluated the impact of the faster and less accurate choices in the small target condition

512 compared to the big target condition on subjects' performance in the tokens task. Because it has

513 been shown that subjects seek to optimize their rate of correct responses rather than their absolute

514 accuracy (Balci et al., 2011), performance is estimated as the duration that subjects needed to

515 complete each motor block. Thus, by calculating the rate of reward and deducting from it the

516 amount of time necessary to complete the different motor blocks in each session (see Methods),

517 we found that this duration was significantly longer in the small target condition compared to the

518 big target condition across subjects, regardless of the session performed, when subjects performed

519 the tokens task in the slow decision block (WMW test, p = 0.0013, Figure 8, left panel). By contrast,

520 we found no significant difference of block duration between small and big target conditions in the

521 fast decision block of trials (WMW test, p = 0.11).

522

523

524 ## DISCUSSION

525   In this study, we assessed whether the motor context in which perceptual decisions between actions

526   are made influences human subjects' decision strategy, as predicted by the recently proposed

527   "shared regulation" hypothesis (Thura et al., 2014). This model conceives decision and action as a

528   continuum, regulated by unspecific signals. As a consequence, a motor context favoring vigorous

529   movements should be preceded by fast decisions because of the activation of one unique

530   invigoration signal possibly computed in the basal ganglia (Cisek and Thura, 2018). We found that

531   motor context indeed often influences decision-making but contrary to the prediction of the shared

532   regulation hypothesis, decisions preceding slow and accurate actions were faster, rather than

533   slower, compared to decisions made in blocks allowing more vigorous and less accurate actions.

534   *Motor costs influence motor and perceptual decision-making*

535   The present results first add to the many recent observations that challenge the classic view of

536   behavior organization, inherited from cognitive psychology, in which perception, decision and

537   action are considered as temporally separate and serial processes (Pylyshyn, 1984). Indeed, in

538   ecological scenarios, sensory or value-based decisions are very often expressed by actions that are

539   themselves associated with risks and costs. For instance, a monkey deciding between reaching

540   toward a grape or a nut may prefer the nut but time and energy expenditure associated with opening

541   its shell may rather encourage him to go for the grape. Because it has been extensively

542   demonstrated that the brain tends to control behavior in such a way that the expected value of a

543   choice is maximized while all types of cost are minimized (Neumann and Morgenstern, 1944;

544   Todorov and Jordan, 2002; Gold and Shadlen, 2007), any potentially penalizing factor, including

545   motor costs, should influence the perceptual judgement leading to a potential reward.

546   In the past decade, several studies have demonstrated that motor costs influence decision-making

547   when choices only rely on movement properties (i.e. motor decisions). Cos and colleagues showed

548   that when humans make rapid choices between reaching actions, they tend to choose the one that

549   carries the lowest biomechanical cost (Cos et al., 2011, 2014). Morel and colleagues found that

550   biomechanics affects action selection too, but among duration, amplitude, direction and force, they

551   observed that movement duration is perceived as the greatest cost by subjects (Morel et al., 2017).

552   Finally, Michalski and colleagues observed that movement amplitude and direction influence the

553   probability of switching from one ongoing movement to another in a common real-life scenario

554   where one has to decide while already acting (Michalski et al., 2020).

555   Other work addressed the effects of motor costs on decision-making beyond purely motor choices,

556   i.e. when the decision primarily relies on perceptual or value information, as in the present work.

557   In three of these experiments using the random dots motion discrimination task, data indicate an

558   effect of motor constraints on non-motor decision-making. Burk and colleagues demonstrated that

559   physical effort affects the proportion of changes of mind made by subjects during the deliberation

560   period: the more the change of mind requires a significant energetic cost, the less subjects are

561   willing to perform it (Burk et al., 2014). Another study showed that asymmetric biomechanical

562   cost biases perceptual decisions, with subjects more systematically choosing targets associated with

563   movements of lower cost, even if these choices were detrimental to accuracy (Marcos et al., 2015).

564   In agreement with this observation, Hagura and colleagues demonstrated that motion

565   discrimination is influenced by the physical resistance applied to the response. Intriguingly, they

566   showed that motor costs also bias vocally-expressed judgments, suggesting that actions changed

567   how subjects perceived the stimuli themselves (Hagura et al., 2017).

568   It is important to note that in these three studies, each of the two potential targets was assigned a

569   specific motor cost during a given choice. By contrast, in the present work, the two targets were

570   always associated with the same motor cost, and that cost was varied between blocks of trials. The

571   present report is thus to our knowledge the first to show that the motor context in which a movement

572   is performed influences the strategy of subjects during decision-making.

573   *A flexible mechanism for regulating decision and movement durations*

574   Decisions about actions typically include a period of deliberation that ends with the commitment

575   to a choice, which then leads to the overt expression of that choice through action execution, at the

576   end of which the reward can be at last consumed. Because decision and action processes are so

577   inextricably linked, it is natural to imagine that they could at least partly share operating principles

578   in order to maximize the utility of behavior. Decision and action could indeed be considered as a

579   continuum during which regulation signals would affect both processes agnostically, in a unified

580   manner. In agreement with this hypothesis, it has been proposed that movement selection,

581   preparation and execution are parameterized following economical rules, varying depending on

582   utility estimation: high valued options lead to faster reaction times and movement speed, and high-

583 perceived effort discount option's value, leading to slower reaction and longer movements

584 (Kawagoe et al., 1998; Wickler et al., 2000; Shadmehr et al., 2010, 2016, 2019; Haith et al., 2012;

585 Choi et al., 2014; Morel et al., 2017; Reppert et al., 2018; Summerside et al., 2018; Yoon et al.,

586 2018; Revol et al., 2019).

587 Our own previous results support this hypothesis of a coordination between decision and action

588 durations during behavior. For instance, within fixed decision and motor contexts, both humans

589 and monkeys shorten their movement duration in trials in which decision duration are prolonged,

590 as if extended deliberation duration was compensated by increasing the action speed so that the

591 next opportunity can be encountered more quickly. Between decision contexts, choices made in a

592 fast speed-accuracy trade-off regime are usually followed by faster movements compared to those

593 made in a regime encouraging slow and accurate choices (Thura et al., 2014; Thura, 2020).

594 Altogether, these observations indicate that the level of urgency at which a decision is made directly

595 influences movement vigor, suggesting that decision and movement durations are determined by

596 a global decision urgency/movement vigor signal that invigorates behavior in order to control

597 reward rate (Cisek and Thura, 2018; Carland et al., 2019). However, a missing test of the shared

598 regulation hypothesis required to vary the motor context in which a decision is made and assess

599 whether or not a motor context permitting execution of vigorous movements to express choices

600 leads to faster decisions compared to the same difficult decisions made in a demanding motor

601 context, imposing slow and accurate movements. Contrary to this prediction, we did not observe a

602 robust and consistent effect of movement speed per se on decision duration and accuracy (by

603 comparing short versus long target conditions, Figure 5B). Instead, data indicate that target size

604 imposes a motor accuracy cost that is tackled by some subjects by shortening the deliberation

605 period (Figure 5A) so that more time is available to prepare the following movement execution.

606 This interpretation is supported by a post-experiment interview during which most of participants

607 declared having consciously expedited and thus "sacrificed" their decisions to better prepare action

608 execution in small target trials. Thus, we demonstrate in the present study that there is no

609 unconditional and unidirectional relationship between action vigor and decision duration, contrary

610 to the prediction of the shared regulation hypothesis. Instead, our results claim for a flexible

611 mechanism in which decision and action durations are regulated by independent, yet interacting,

612 decision urgency and movement vigor signals. Such a flexibility is certainly advantageous given

23

613   the inherent complexity of the many variables interrelationships at play during goal-directed

614   behavior, where no single decision policy is guaranteed to maximize reward rate across all contexts.

615   Such flexibility is well illustrated by the relationship between the effect of target size on decision

616   duration in the tokens task and the effect of target size on reaction time in the delayed reach (DR)

617   task. The significant correlation (Figure 6) indicates that subjects who are slower to initiate a

618   movement in the small target trials of the DR task are also the subjects who adjust their decision

619   policy the most in these difficult trials in the tokens task. The former result is consistent with data

620   suggesting that effortful movements discount reward value, thus motivation, delaying the initiation

621   of movements (Summerside et al., 2018; Shadmehr et al., 2019). This relationship thus suggests

622   that economic principles governing behavior utility in non-decision tasks extends to decision-

623   making. It also indicates that when the task difficulty mainly relies on movement execution, as in

624   the DR task, movement effort slows down reaction times whereas when task difficulty is shared

625   between decision and action, as in the tokens task, movement effort influences the decision process

626   in an opposite way. What could be the relevance of this intriguing behavior in terms of

627   performance?

628   *Impact of a demanding movement on reward rate*

629   The present data indicate that movement accuracy requirement, more than speed or duration, forced

630   some subjects to hasten their decisions. It seems that they took advantage of the potentially long

631   deliberation period permitted in the task (up to 3s) to sometimes shorten their judgment in order to

632   focus on the following movement execution. Interestingly, such adjustment only occurred in blocks

633   of trials in which decisions were encouraged to be conservative ("slow" decision blocks, Figure 7).

634   Indeed, the large and very profitable, in terms of reward rate, shortening of decision durations

635   observed in the "fast" decision blocks (Figure 8) probably constrained decision policy too much,

636   preventing any other adjustments of behavior. It is also important to remember that in the tokens

637   task, deciding more quickly does not provide additional time to execute the movement, the

638   maximum movement duration being fixed at 800ms regardless of subjects' reach onset timing.

639   How then can one explain this suboptimal strategy? One possibility is that our limited cognitive

640   and motor resources imposed a necessary trade-off between decision and action when task

641   constraints were too demanding (Wickens, 2002). In this view, subjects had to choose between

642   allocating ressources on decision-making while taking the risk of producing inaccurate movements

643   or rather sacrificing decision-making to presumably better prepare and execute their movements.

644   Knowing that in ecological situations as in the present task, a movement usually follows the

645   decision, it is possible that subjects gave priority to the action process considering that movement

646   failure would prevent reward acquisition even if the decision was correct. Although it may be

647   advantageous in terms of reward rate to decide very quickly while sacrificing a little bit of precision

648   (see equation 3), as observed when humans and monkeys decide faster in the fast compared to the

649   slow decision block of trials (Figure 8 and Thura et al., 2014; Thura, 2020), our results show

650   however that the strategy consisting of sacrificing decision accuracy to execute accurate

651   movements led to a drop of reward rate compared to a condition in which such adjustment was not

652   necessary. This is probably because in small target trials, the probability of choosing the correct

653   target decreased, even if the amount of time saved during the deliberation period compensated the

654   longer movements made in this condition (Figure 4).

655   *Possible neurophysiological origin of the decision and action regulation mechanism*

656   The interaction between the decision and action regulations provides a clue to the neural origins of

657   the signals implicated in this mechanism. Interacting decision urgency and movement vigor signals

658   would be expected to originate from a region that projects to a wide range of cortical areas to

659   influence both decision-making and action execution. In this respect, the basal ganglia (BG)

660   provide a natural candidate. The BG have long been functionally associated with the regulation of

661   motivated behavior and reinforcement learning for maximizing reward (Graybiel, 2005; Frank,

662   2011), and multiple lines of neuropsychological, neurological and neurophysiological evidence

663   suggest that effort expenditure and movement vigor are largely under the control of activity within

664   a variety of BG structures, including the striatum, substantia nigra, ventral pallidum, and the globus

665   pallidus (Mazzoni et al., 2007; Turner and Desmurget, 2010; Rueda-Orozco and Robbe, 2015;

666   Dudman and Krakauer, 2016; Thura and Cisek, 2017; da Silva et al., 2018; Yttri and Dudman,

667   2018; Carland et al., 2019; Fobbs et al., 2020). All these studies along with results from the present

668   report suggest a mechanism in which different populations of cells, located in the BG output nuclei,

669   vary their activity to adjust both decision and motor durations under specific circumstances, in

670   order to control the rate of reward. Future experiments designed to record activity of individual BG

671   cells during decision-making between actions in different decision and motor contexts should allow

672   to better understand the neural correlates of this regulation mechanism.

673

674   *Limitations*

675   A limitation of the present study, as often in investigations of primate cognition and behavior,

676   relates to the between-subject variability of the results. The average decision duration ranges from

677   ~700ms to about 1600ms depending on subjects (Figure 5), despite the fact that participants faced

678   the same trials under identical conditions. This indicates individual "traits" of decision behavior.

679   Similarly, a subgroup of four subjects were more vigorous than the others to execute their

680   movements (Figure 4). While revealing probable unaddressed phenomena, these multiple levels of

681   variability are still compatible with a flexible regulation mechanism of decision and action

682   durations that would be idiosyncratic in nature. Another limitation relates to the absence of decision

683   data analysis in inaccurate or slow movement trials for methodology reasons. In the present report

684   we show that a difficult movement is often preceded by a fast and inaccurate decision, but this

685   occurs when movements are properly executed. It is possible that subjects sometimes allocated

686   their attention on the decision process, leading in that case to a "sacrifice" of motor control,

687   resulting in failed movements. Further experiments or analyses are needed to reveal which of the

688   two processes, the decision or the action, is typically prioritized by participants in this kind of

689   demanding goal-directed behavior.

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694   ACKNOWLEDGMENTS

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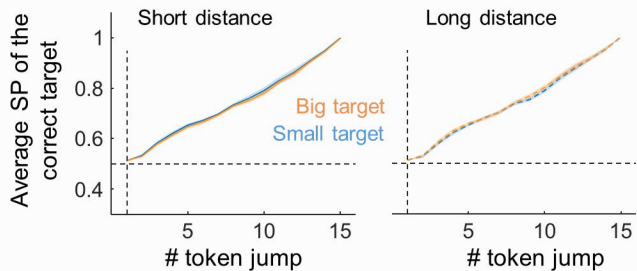796   956.

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A

Time
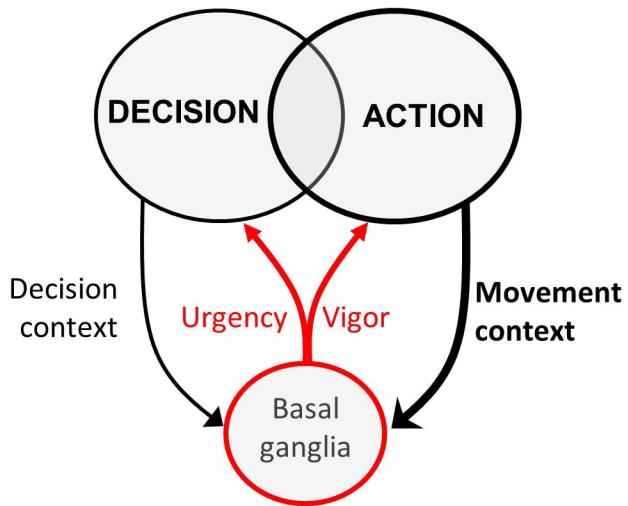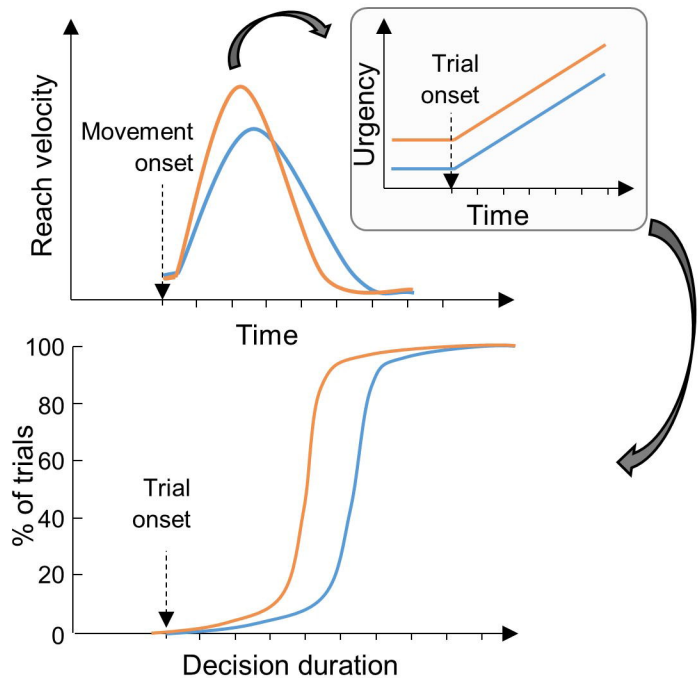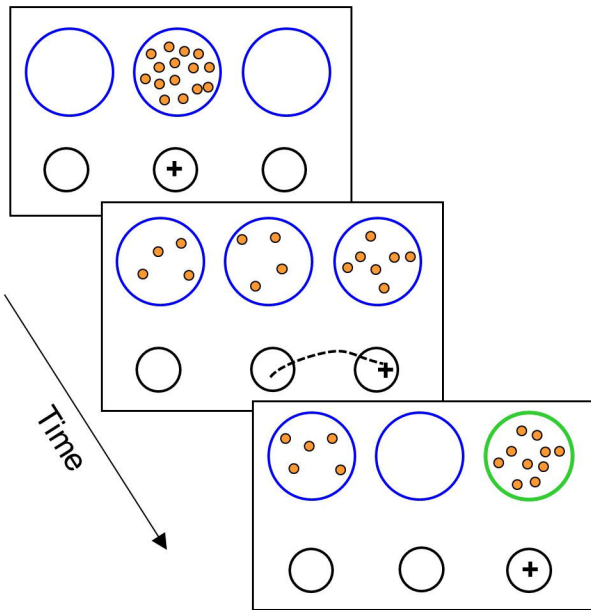
B

4 motor blocks:

— Small & short targets   — Big & short targets
···· Small & long targets   ···· Big & long targets

C

Short distance

Long distance

Average SP of the correct target

Big target
Small target

token jump

token jump
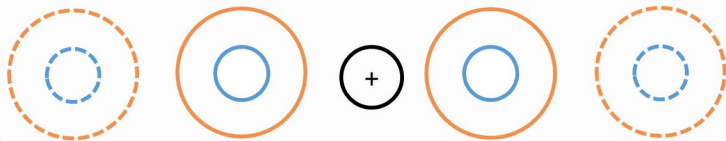
A

Subject S6

Small-short block   Small-long block   Big-short block   Big-long block

Vertical position (cm)

Horizontal position (cm)

B

Subject S6

Reach velocity (cm/s)

Time from movement onset (s)
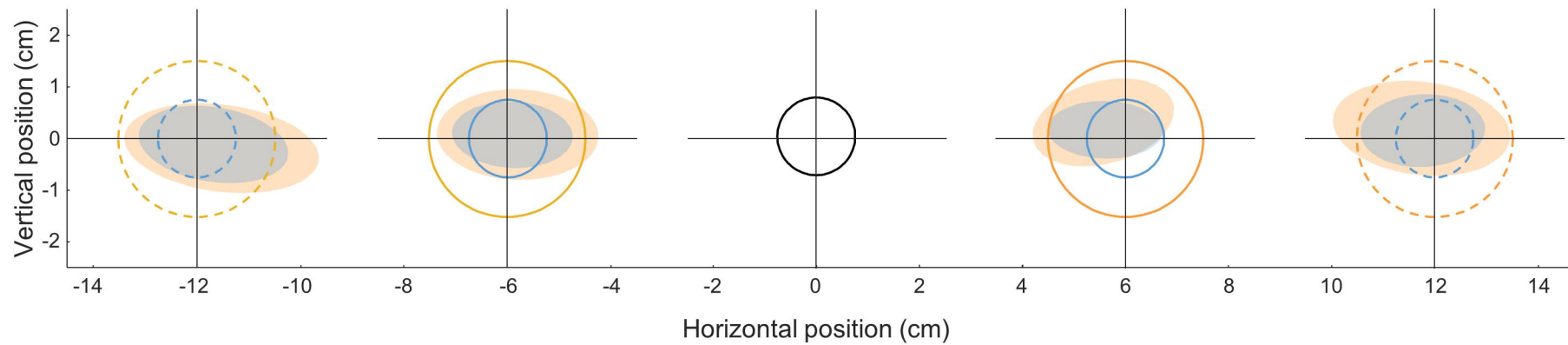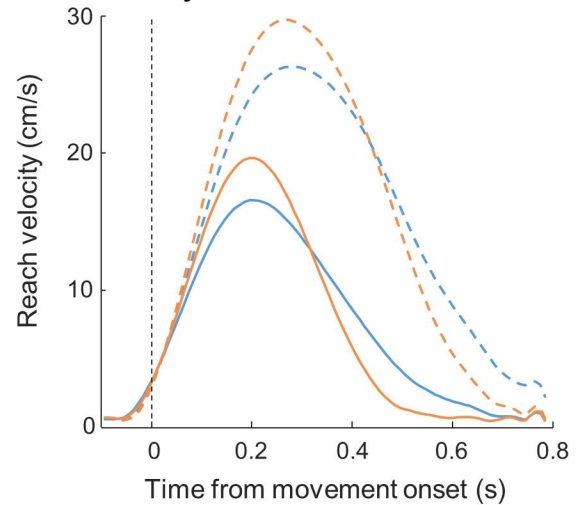
Tokens task
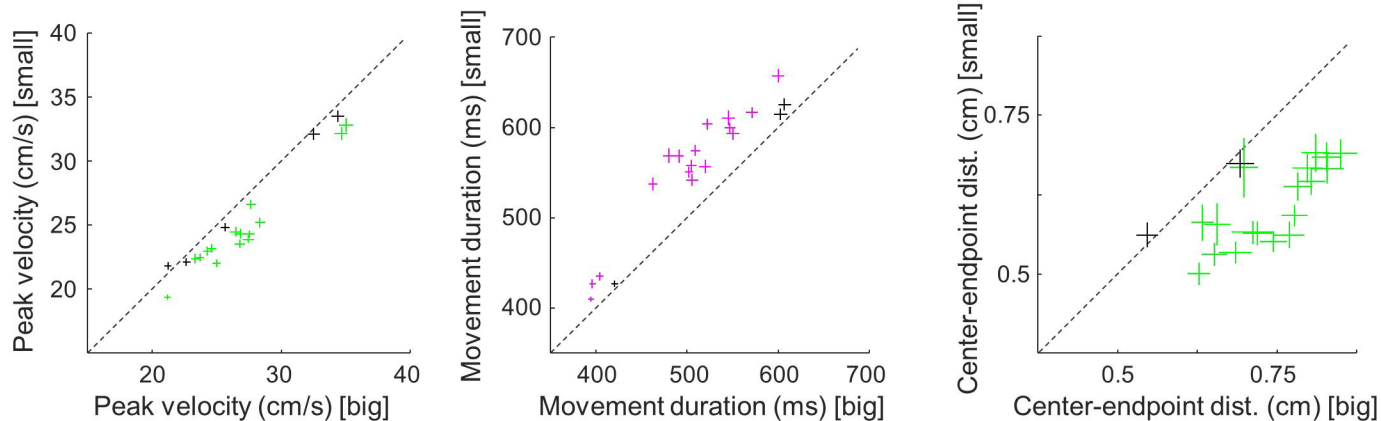
A *Size contrast*

B *Distance contrast*
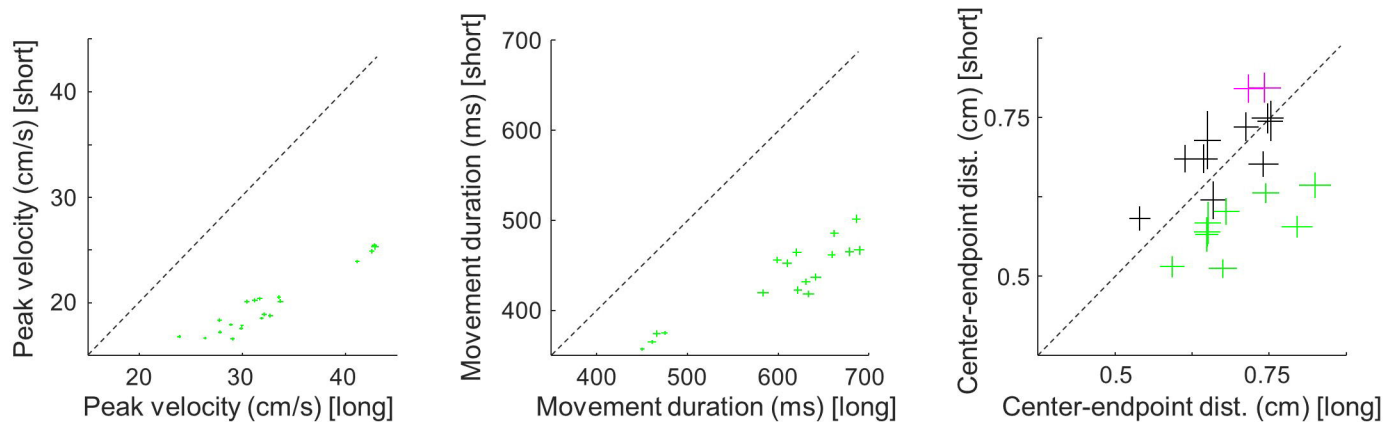
Tokens task

A *Size contrast*
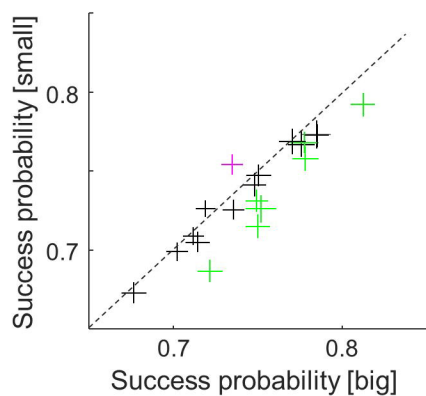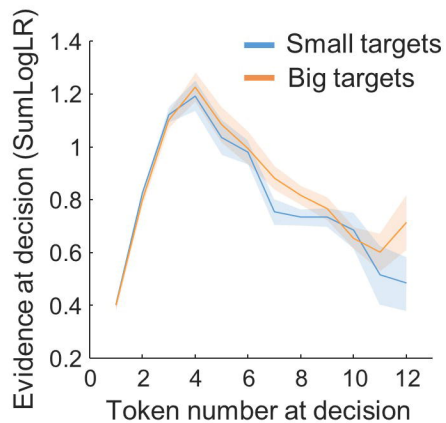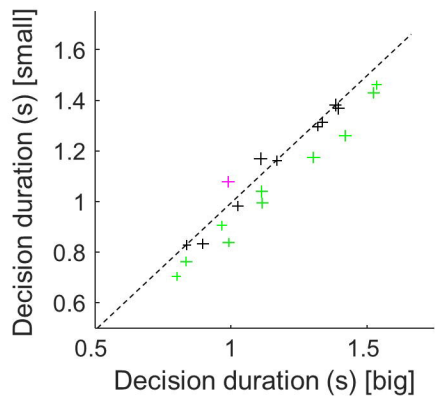
B *Distance contrast*
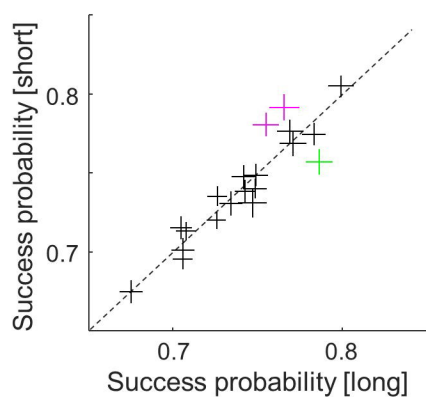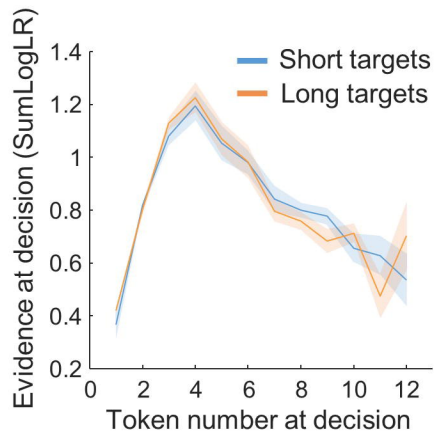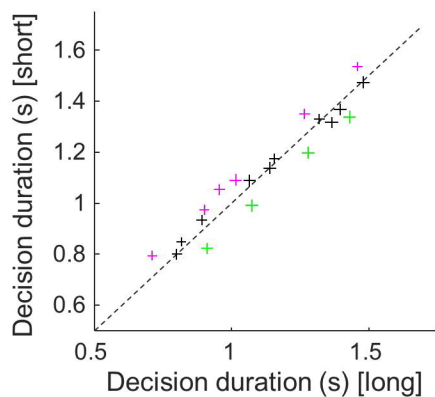
DR task

C *Size contrast*
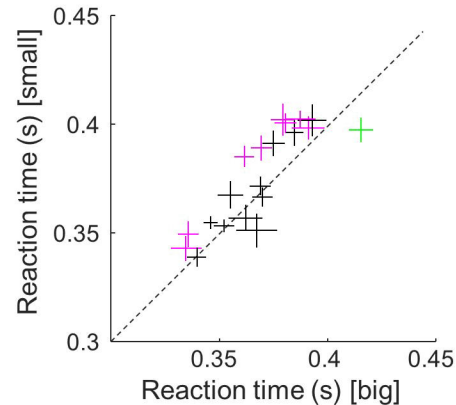
D *Distance contrast*

Size contrast

ΔRT small – big (ms)

ΔDD small – big (ms)

r = -0.495; p=0.03

Distance contrast

ΔRT short – long (ms)

ΔDD short – long (ms)

r = -0.34; p=0.14
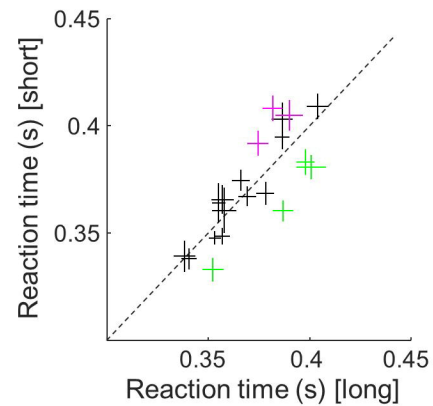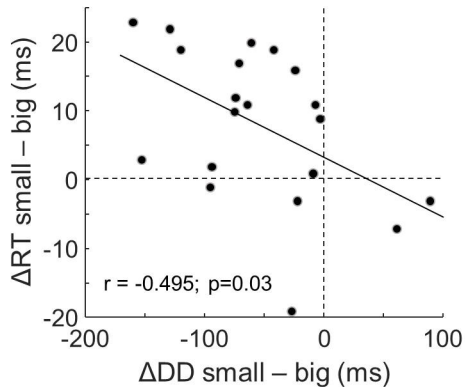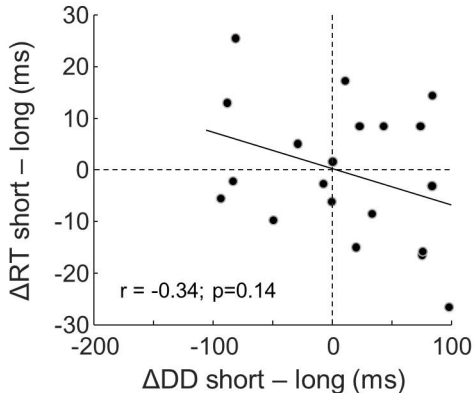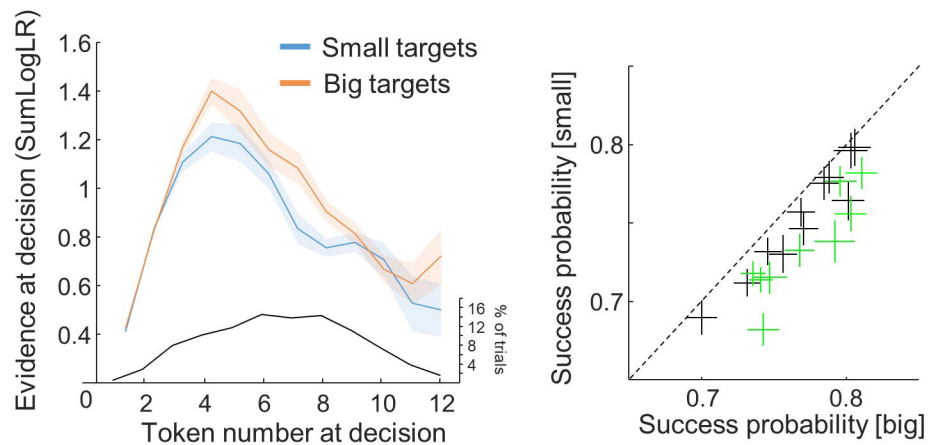
A *Slow block*

B *Fast block*

C *Session #1*

D *Session #2*