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# 1 Decision urgency invigorates movement in humans

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23

24 **ABSTRACT**

25 Recent work in highly trained monkeys suggests that decision-making and motor control are  
26 linked processes whose regulation by urgency allows reward rate optimization. However, such  
27 urgency-based mechanism might be species-specific and/or a consequence of practice. Here I  
28 show that the unified regulation hypothesis exists in naïve human subjects. Seventeen volunteers  
29 performed a reach decision task in which blocks of trials encouraged either risky or conservative  
30 choices. Participants performed at least two sessions in which they were indirectly motivated to  
31 maximize their reward rate. Results show that subjects' accuracy criterion decreased over time  
32 within each trial, and that decisions were earlier and less accurate in fast than slow blocks, with a  
33 larger difference in session #2 compared to session #1. A simple model in which sensory  
34 information is combined with a growing urgency signal captured these effects. Crucially, arm  
35 and eye movement vigor systematically increased as decision duration increased within blocks  
36 and the block-dependent decision policy strongly predicted the kinematics of reaching  
37 movements. These results suggest a practice-independent mechanistic link for establishing the  
38 unified control of human decision timing and action vigor in order to optimize the rate of reward.

39

40 **KEYWORDS**

41 Decision-Making, Reaching, Reward Rate, Urgency, Practice, Human

42

43 **1. INTRODUCTION**

44 Decision-making is ubiquitous in animal kingdom. The type of decisions humans share with  
45 other animals is mainly restricted to decisions between actions, whether these decisions rely on  
46 purely sensory or on combined value-sensory cues. Crucially, neural circuits underpinning  
47 decisions between actions have been remarkably conserved through evolution. For instance,  
48 animals as old as lampreys possess the same basal ganglia machinery, in terms of connectivity,  
49 ion channels, transmitters and co-transmitters, as mammals (1,2).

50 Most recent theoretical and experimental work suggests that action selection and execution are  
51 tightly linked processes that share neural substrates (3,4). This “embodied” decision concept (5,6)  
52 diverges from the classical view, inherited from cognitive psychology, in which perception,  
53 decision and action are considered as temporally separate and serial processes (7,8). Embodied  
54 decision-making makes very good ecological sense: options are always multiple, specified by  
55 spatio-temporal information and highly dynamic in nature (9). Consequently, the mechanisms  
56 that serve decisions made during interactive behavior must have been designed to be very fast  
57 and flexible. For instance, individuals are free to adjust the time they invest in deciding versus  
58 moving. This is crucial because the actual subjective value of a given activity is not only  
59 determined by the immediate rewards and efforts associated with that activity but also by the  
60 amount of time invested in it. Therefore, what is ultimately most adaptive is to choose actions  
61 that maximize one’s global reward rate (10,11), which occurs when the decision and action  
62 processes are sufficiently accurate but not overly time consuming. Thus, nearly all decision  
63 scenarios present decision-makers with a speed-accuracy trade-off (SAT) *during both decision*  
64 *and action.*

65 Thenceforth, how to determine the deliberation duration and the movement speed that optimize  
66 reward rate? On one hand, my colleagues and I, among others, have proposed that control of  
67 decision urgency is critical for reward rate maximization (12–17). Urgency is a context-  
68 dependent, motor-related signal that grows over the time course of a deliberation. It pushes the  
69 decision-related neural activity toward the commitment threshold, thus preventing spending too  
70 much time on a choice when sensory evidence is weak and outcome uncertain (18,19). On the  
71 other hand, it has been convincingly shown that movement properties are determined according  
72 to economical rules, showing modulations of vigor and variability depending on reward  
73 probability and delay (20–24). My previous work also demonstrated that, in trained monkeys,  
74 urgency not only controls decision-making timing, but also the speed of the following motor  
75 commands: reaching movements expressing urgent decisions were faster compared to  
76 movements expressing informed, evidence-based decisions. Interestingly, the urgency effect on  
77 movement execution did not appear to be effector-specific, as it also affected to some extent the  
78 speed of saccadic eye movements, despite the fact that oculomotor behavior was not constrained  
79 in the task and did not affect reward rate (25,26).

80 Consistent with a role in the simultaneous modulation of multiple processes, it has been proposed  
81 that the neural correlates of the urgency signal lie in the basal ganglia (27–29), a set of  
82 subcortical nuclei forming segregated neuroanatomical loops with nearly every parts of the brain.  
83 Accordingly, urgency might provide a mechanistic link for establishing the unified control of  
84 both decision timing and action vigor in order to optimize reward rate through projections from  
85 the basal ganglia to sensorimotor regions (25,30,31). More globally, urgency might also play a  
86 key role in a wide variety of phenomena in both health and disease, ranging from personality  
87 traits such as impulsivity or apathy, to major pathological conditions such as in Parkinson's

88 disease or obsessive compulsive disorders, through projections to other cortical regions, including  
89 prefrontal and limbic areas (32–34).

90 However, most of the arguments in support of a role of urgency in goal oriented-behavior rely on  
91 data collected on highly trained monkeys who performed the same decision-making tasks for  
92 months or even years. This is a concern because some findings suggest that human and non-  
93 human primates adopt different policies to make rapid decisions between actions (see for instance  
94 (35,36)). One possible explanation for this discrepancy is that decision mechanisms are truly  
95 species-specific, only permitting the species-dependent strategies that produced the behavioral  
96 differences observed in the literature. In agreement with this possibility, recent quantitative  
97 analyses of human behavior have found evidence in favor of urgency-free mechanisms of  
98 decision-making (37,38), whereas research comparing urgency versus urgency-free mechanisms  
99 in non-human primates has provided convincing support for an urgency-based decision  
100 mechanism (35,39). Another possibility is that, because monkeys are usually trained on a  
101 behavioral task over a long period of time, the large amount of practice shapes their behavior,  
102 allowing them to explore more strategies than human subjects faced with only a few experimental  
103 sessions. As a consequence, a debate recently emerged in the field in which it has been  
104 legitimately argued that urgency-based mechanisms may only be present in naturally “impatient”  
105 species like monkeys, or in highly trained individuals (11,35,36,39,40).

106 The aim of the present work was thus to test the hypothesis that the common regulation of  
107 decision and movement durations by urgency which has been previously observed in “expert”  
108 monkeys is not species-specific, nor a consequence of overtraining. This hypothesis predicts that  
109 naïve human subjects will adopt urgency-based decision policy as soon as they will perform their  
110 first experimental session and that this policy will modulate the way they express their choices

111 via reaching movements. It also predicts that decision urgency will influence movements that do  
112 not directly influence reward rate, such as saccades, in the task described below.

113 To this aim, I conducted an experiment where participants performed a reach decision task in  
114 which (1) deliberation duration is controlled by subjects and is dissociated from commitment  
115 time, allowing an accurate investigation of these two distinct processes, including the  
116 quantification of the sensory information used by subjects at time of commitment and the  
117 inference of the urgency level at that time; (2) sensory information continuously evolves during  
118 the time course of a trial, an ecological feature allowing to make distinct predictions about the  
119 decision mechanism involved (see (15,18)); (3) the timing parameters can be manipulated in  
120 order to encourage speed-accuracy trade-off adjustments, allowing to test the effect of such SAT  
121 context on decision and movement policies; (4) decisions are expressed with reaching  
122 movements and oculomotor behavior is unconstrained, allowing to assess the effect of decision  
123 policy on motor control.

## 124 **2. MATERIALS AND METHODS**

### 125 *2.1 Participants*

126 Twenty healthy, human subjects (ages: 18-41; 14 females; all right handed) participated in this  
127 study. All gave their consent before starting the experiment. The ethics committee of Inserm  
128 (IRB00003888) approved the protocol on March 19<sup>th</sup> 2019. Each participant was asked to  
129 perform two experimental sessions. They received a monetary compensation (20 euros per  
130 completed session) for participating in this study. Among them, seventeen (ages: 20-41; 13  
131 females) completed at least two sessions and have thus been included in the present dataset.

### 132 *2.2 Setup*

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

134 right hand. A digitizing tablet (GTCO CalComp) continuously recorded the lever horizontal and  
135 vertical positions (125 Hz with 0.013cm accuracy). Target stimuli and cursor feedback were  
136 projected by a DELL P2219H LCD monitor (60 Hz refresh rate) onto a half-silvered mirror  
137 suspended 26 cm above and parallel to the digitizer plane, creating the illusion that targets floated  
138 on the plane of the tablet. Unconstrained eye movements and pupil area were recorded using an  
139 infrared camera (ISCAN, sampling rate of 120 Hz).

### 140 *2.3 Tasks*

141 The subjects performed a modified version of the tokens task (Figure 1A, 41). They were faced  
142 with a visual display consisting of three blue circles (1.5 cm radius) placed horizontally at a  
143 distance of 6 cm of each other (the “decision” stimuli). In the central blue circle 15 small tokens  
144 were randomly arranged. Positioned 12 cm below, three black circles, organized horizontally as  
145 well, defined the “movement” stimuli. While the central black circle radius was kept constant at  
146 0.75 cm, the size of the lateral black circles and their distance from the central circle could vary  
147 in blocks of trials: Size was set to be either 0.75 or 1.5 cm of radius, and distance from the central  
148 circle was varied to be either 6 or 12 cm (see below).

149 A trial was initiated when the subject moved the lever into the small black central circle (starting  
150 position) and stayed immobile for 500ms. At this time the tokens started to jump, one by one,  
151 every 200ms in one of the two possible lateral blue circles. The subjects’ task was to decide  
152 which of the two lateral blue circles would receive the majority of the tokens at the end of the  
153 trial. They reported their decisions by moving the lever into the lateral black circle corresponding  
154 to the side of the chosen blue circle. Importantly, subjects were allowed to make and report their  
155 choice at any time between the first and the last jump. Arm movement duration could not exceed  
156 800ms, preventing overtly expressed changes of mind. Once the choice was reported, the



157 remaining tokens jumped more quickly to their final targets. In separate blocks of trials, this post-  
158 decision interval was set to either 20ms (“fast” blocks) or to 150ms (“slow” blocks). After  
159 holding the lever in the target for 500ms, a visual feedback about decision success or failure (the  
160 chosen decision circle turning either green or red, respectively) was provided after the last token  
161 jump. A 1500ms period (the inter-trial interval) preceded the following trial.

162 Before and after the tokens task described above, each subject also performed 100 trials (2 blocks  
163 of 25 trials before and 2 blocks of 25 trials after the tokens task) of a simple choice, delayed  
164 reaction time task (DR task). This task was identical to the tokens task except that there was only  
165 one lateral decision circle displayed at the beginning of the trial (either at the right or at the left  
166 side of the central circle with 50% probability) and all tokens moved from the central circle to  
167 this unique circle at a GO signal occurring after a variable delay ( $1000 \pm 150$ ms). This task was  
168 used to estimate of the sum of the delays attributable to sensory processing of the stimulus  
169 display as well as to response initiation.

#### 170 *2.4 Instructions*

171 In a given session, subjects were asked to complete one slow block and one fast block of the  
172 tokens task. To complete a block, subjects had to make 160 correct choices, indirectly motivating  
173 them to optimize successes per unit of time. After the first block completed, a short break was  
174 offered to the subject. Within each block, the size of the movement targets and their distance  
175 from the starting circle were varied every 40 trials. The influence of the reaching target properties  
176 on subjects’ behavior is not described in the present paper.

177 In order to test the effect of practice on decision/movement policy, subjects performed two  
178 sessions (test-retest design), one per day and each of them separated by a maximum of seven  
179 days. In session #1 subjects first performed the tokens task in the slow block, followed by the fast

180 block. To prevent any block-related confounding effect, the order of block presentation was  
181 reversed in session #2. Before the first session, I explicitly described to the subjects the principle  
182 of each block, specifying that deciding quickly in the fast block was more advantageous in terms  
183 of time saving than in the slow block (because of the larger acceleration of the remaining tokens)  
184 but that hasty behavior could also lead to more erroneous decisions. Subjects were thus informed  
185 that they could volitionally adjust their behavior depending on the block condition but they were  
186 not penalized for behaving exactly the same way in the two blocks. A short recall was provided  
187 before starting the second session. Because subjects were informed that they had to complete a  
188 given number of correct responses, they were all aware that they were presented with a  
189 speed/accuracy trade-off in this task.

190 A “familiarization” period consisting of performing 20 tokens task trials was proposed at the  
191 beginning of the first session, mainly allowing subjects to get familiar and comfortable with the  
192 manipulation of the lever on the tablet.

193 Among the 21 subjects who participated in this study, two have been tested six and seven times,  
194 still performing one session a day with no more than seven days between two successive  
195 sessions. For these two “longitudinal” subjects, the order of block presentation was varied before  
196 each new session.

### 197 *2.5 Data analysis*

198 The tokens task allows to calculate, at each moment in time, the success probability  $p_i(t)$   
199 associated with choosing each target  $i$ . For instance, for a total of 15 tokens, if at a particular  
200 moment in time the right target contains  $N_R$  tokens, whereas the left contains  $N_L$  tokens, and there  
201 are  $N_C$  tokens remaining in the center, then the probability that the target on the right will  
202 ultimately be the correct one (i.e., the success probability of guessing right) is as follows:

203

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

204 To characterize the success probability profile for each trial, I calculated this quantity (with  
205 respect to the target ultimately chosen by the subject) for each token jump (Fig. 1B). All subjects  
206 faced the same sequence of trials, in which I interspersed among fully random trials (20% of the  
207 trials in which each token is 50% likely to jump into the right or into the left lateral circle) three  
208 special types of trials characterized by particular temporal profiles of success probability.  
209 Subjects were not told about the existence of these trials. 30 % of trials were so-called “easy”  
210 trials, in which tokens tended to move consistently toward one of the circles, quickly driving the  
211 success probability  $p_i(t)$  for each toward either 0 or 1. There were several variations of easy trials  
212 (see the criteria in Figure 1C), and the average success probability profile is shown in Figure 1C  
213 (green curve). Another 30% of trials were “ambiguous” (Fig. 1C, blue-green curve), in which the  
214 initial token movements were balanced, making the  $p_i(t)$  function close to 0.5 until late in the  
215 trial. The last special trial type was called “misleading” trials (20%) in which the 2-3 first tokens  
216 jumped into the incorrect circle and the remaining ones into the correct circle. In all cases, even  
217 when the temporal profile of success probability of a trial was predesigned, the actual correct  
218 target was randomly selected on each trial.

219 To estimate the time at which subjects committed to their choice (decision time, DT) on each trial  
220 in the tokens task, I detected the time of movement onset (based on reach kinematics, defining  
221 subject’s reaction time, RT) and subtracted the subject’s mean sensory-motor delays (SM)  
222 estimated from the DR task performed on the same day. Decision duration was computed as the

223 duration between decision time and the first token jump. I then used Equation 1 to compute for  
224 each trial the success probability at the time of the decision (SP; Fig. 1B).

225 To quantify subjects' performance, I first calculated the reward rate (RR), using a local definition  
226 (15,22) which corresponds to the expected number of correct choices per unit of time. This is  
227 computed as follows:

228

$$RR_n = \frac{SP_n}{DT_n + SM + MT_n + RD_n + ITI} \quad (2)$$

229 where  $SP_n$  is the probability that the choice made on trial  $n$  was correct,  $DT_n$  is the time taken to  
230 make the decision,  $SM$  is the sensori-motor delays (constant for a given session),  $MT_n$  is the  
231 movement time,  $RD_n$  is the duration of the remaining token jumps after the target is reached, and  
232  $ITI$  is the inter-trial interval (fixed at 1500ms). Then from the average reward rate computed in  
233 each block I calculated the average number of correct choices per minute and deducted from it  
234 the time necessary to complete 160 correct choices in each of the slow and fast conditions.

235 Calculation of subjects' accuracy criterion at decision time relies on the available sensory  
236 evidence at that time. Because it is very unlikely that subjects can calculate Equation 1, I  
237 computed a simple "first order" approximation of sensory evidence as the sum of log-likelihood  
238 ratios (SumLogLR) of individual token movements as follows (41, page 11567, provides more  
239 details on this analysis):

$$SumLogLR(n) = \sum_{k=1}^n \log \frac{p(e_k|S)}{p(e_k|U)} \quad (3)$$

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

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

247 All arm and eye movement data were analyzed off-line using MATLAB (MathWorks). Reaching  
248 characteristics were assessed using subjects' movement kinematics. Horizontal and vertical  
249 position data were first differentiated to obtain a velocity profile and then filtered using a sixth  
250 order low-pass filter with a frequency cutoff of 15 Hz. Onset and offset of movements were  
251 determined using a 3 cm/s velocity threshold. Peak velocity was determined as the maximum  
252 value between these two events. Reaching movement vigor was estimated by dividing the  
253 movement peak velocity by its amplitude. Therefore, according to this local definition, a  
254 movement is more vigorous than another if for the same amplitude, its peak velocity is higher.

255 During both the tokens and the DR tasks, subjects eye movements were unconstrained. After  
256 each session, an offline recalibration of the raw eye position signals was performed (taking the  
257 average eye position in the DR task as a reference), after which eye data were first differentiated,  
258 filtered using a sixth-order low-pass filter with a frequency cut-off of 50 Hz and then up-sampled  
259 at 1000 Hz using a cubic spline interpolation method. The beginning and end of saccades were  
260 identified using an adaptive velocity threshold algorithm (varying as a function of the signal-to-  
261 noise ratio). Because the two decision circles were arranged horizontally from each other, most  
262 saccades were mainly horizontal during the deliberation process. I thus only analyzed the  
263 horizontal component of saccades made by subjects during the deliberation period. Moreover, to  
264 be included in the analyses, saccades had to have an amplitude between 20 and 34 degrees of

265 visual angle (corresponding to saccades made between the two lateral circles), a peak velocity  
266 between 400 and 900 degrees/s, a duration above 50ms, and be executed after the first token  
267 jump and before the estimate of the subject's decision time.

## 268 *2.6 Computational modeling*

269 Mathematically, an urgency-based decision mechanism can be implemented in different ways,  
270 but the best match between the neurophysiological data and model predictions is provided by a  
271 short-time constant integration process with a gain of the sensory signals, which increases over  
272 time during deliberation (18,41). To simulate the decision data, I thus used a minimal  
273 implementation of the urgency gating model (15,41), in which evidence is multiplied by a  
274 linearly increasing urgency signal, and then compared with a fixed threshold. This mechanism  
275 roughly corresponds to a threshold that continuously collapses over the time course of a decision  
276 while sensory gain is kept stable. Because in the present task there is no stimulus noise, I  
277 discarded the low-pass filtering stage of the sensory evidence and calculated it simply as the  
278 difference in the number of tokens in each target (25). The result can be expressed as follows:

$$y_i = (N_i - N_{j \neq i}) \cdot [mt + b]^+ < T \quad (4)$$

279 where  $y_i$  is the “neural activity” for choices to target  $i$ ,  $N_i$  is the number of tokens in target  $i$ ,  $t$  is  
280 the number of seconds elapsed since the start of the trial,  $m$  and  $b$  are the slope and y-intercept of  
281 the urgency signal, and  $[\ ]^+$  denotes half-wave rectification (which sets all negative values to  
282 zero). When  $y_i$  for any target crosses the threshold  $T$ , that target is chosen. Two sources of  
283 internal variability were introduced into the model. Inter-trial variability was simulated by  
284 multiplying the urgency signal by a factor that was normally distributed with mean = 1 and SD =  
285 0.1. Intra-trial variability was simulated by jittering the decision time by a term that was normally  
286 distributed with mean zero and SD of 0.2 s.

287 This simple model has only two free (but constrained, see below) parameters:  $m$  and  $b$  (the  
288 threshold  $T$  is just a scaling factor). To fit the data, I set  $T = 1$  and then performed an exhaustive  
289 grid search for all (2050) combinations of  $m$  and  $b$  where  $m$  ranged from 0 to 0.40, and  $b$  ranged  
290 from -1.2 to 0.76. This was performed separately for each block type, with data combined across  
291 all trials, and the quality of fit was assessed using the mean-squared-error between the sum of  
292 log-likelihood ratios as a function of time (Equation 3) generated by the model and data for all  
293 decision times in the interval between 0 and 3.0s. After finding the best pair of parameters for  
294 each dataset using the grid search, I performed a bootstrap consisting of randomly picking trials  
295 with replacement among the original dataset within each block to determine a new best pair of  
296 parameters with the grid search method. After repeating this procedure 500 times, I computed the  
297 mean shape (linear function based on  $m$  and  $b$  parameters)  $\pm$  SD of the urgency functions from  
298 the best parameters distribution.

299 Thus, contrary to most investigations of SAT control in which the threshold value differs between  
300 SAT conditions, here the decision threshold is fixed and the variation of the context-dependent  
301 distance between the starting point and this threshold is captured by adjustments of the urgency  
302 signal, both between and within blocks of trials.

### 303 **3. RESULTS**

#### 304 *3.1 Global performance*

305 In the tokens task, the overall percentage of correct choices of subjects performing the first  
306 session was  $79\% \pm 4.9$  (slow block:  $80\% \pm 5.7$  – range: 68-86%; fast block:  $78\% \pm 5.3$  – range:  
307 66-85%). Their performance slightly increased during the second session:  $81\% \pm 4.0$  (slow block:  
308  $83\% \pm 3.3$  – range: 73-87%; fast block:  $80\% \pm 5.4$  – range: 71-91%).

#### 309 *3.2 Decision duration and success probability*

310 As expected, subjects' behavior was strongly influenced by the specific pattern of token  
311 movements within a trial (i.e. trial difficulty), regardless of the session or the block condition. As  
312 a typical example, Figure 2A,B shows decision durations and success probabilities of a subject  
313 faced with easy and ambiguous trials during the tokens task. Decisions were faster and success  
314 probabilities higher in easy trials compared to ambiguous trials (Wilcoxon-Mann-Whitney test,  
315  $p < 0.0001$  for all comparisons).

316 During their first session, the majority of subjects did not behave differently (in terms of decision  
317 duration and success probability) in the slow and the fast blocks of trials. Decision durations and  
318 probabilities of success were not statistically different between the blocks in 9 and 10 out of 17  
319 subjects, respectively (Fig. 2C, WMW test,  $p < 0.05$ ). By contrast, in sessions #2, the vast majority  
320 of subjects decided faster (14/17) and with a lower probability of success (13/17) in the fast block  
321 compared to the slow block, as shown in Figure 2C (WMW test,  $p < 0.05$ ). Figure 2B shows this  
322 effect for a typical subject in easy and ambiguous trials (compare top and bottom panels). It is  
323 interesting to note that this adjustment of behavior between the two sessions consisted in an  
324 increase of decision durations, mainly in the slow block, leading to the largest difference of  
325 decision duration and success probability between the blocks in sessions #2 compared to sessions  
326 #1 (average durations at the population level in slow versus fast blocks: 1103ms versus 962ms in  
327 sessions #1 and 1277ms versus 1012ms in sessions #2, Fig. 2D).

### 328 *3.3 Sensory evidence at commitment time*

329 To estimate the amount of sensory evidence the subjects needed to commit to their choices (i.e.  
330 their accuracy criterion), I computed the sum of the log-likelihood ratios (SumLogLR) at decision  
331 time, indicating the available sensory evidence for the chosen target at the time of the decision  
332 (see 4.1 and 2.5 in Materials and Methods), as a function of decision duration for the two block



333 conditions and for the two sessions separately (Fig. 3A). On average, the accuracy criterion of  
334 subjects performing their first session was significantly higher during slow blocks than fast  
335 blocks (ANCOVA, SumLogLR, block effect,  $F_{(1,345)}=5.93$ ,  $p=0.02$ ). This difference was  
336 increased during sessions #2 (SumLogLR, block effect,  $F_{(1,332)}=30.26$ ,  $p<0.001$ ), especially for  
337 decisions made between the fourth and the 9th token jump, i.e. the majority of decisions: 80%  
338 and 74% of slow and fast decisions, respectively (SumLogLR, block effect,  $F_{(1,198)}=52.2$ ,  
339  $p<0.001$ ). This indicates that the subjects were more willing to tolerate less sensory evidence to  
340 make their choices in the fast blocks compared to the slow blocks. I also found that except for  
341 very fast decisions ( $<800$ ms), the level of sensory evidence that subjects required before  
342 committing to a choice decreased as a function of decision duration, in both blocks and in both  
343 sessions (SumLogLR, time effect,  $F_{(1,266)}=62.8$ ,  $p<0.001$  in sessions #1;  $F_{(1,271)}=159.3$ ,  $p<0.001$  in  
344 sessions #2). Crucially, the difference of accuracy criterion between the blocks performed in  
345 sessions #2 was large and robust between subjects for decisions ranging from 800 to 1400ms and  
346 then tended to vanish for longer choices (SumLogLR, block x time interaction,  $F_{(1,271)}=6.8$ ,  
347  $p=0.01$ ). Figure 3B illustrates this phenomenon for each subject by comparing the average  
348 available sensory evidence at decision time between blocks when they decided after 4 or 10 token  
349 jumps. This “converging” effect was not observed for data collected in sessions #1 (SumLogLR,  
350 block x time interaction,  $F_{(1,266)}=0.18$ ,  $p=0.67$ ).

### 351 *3.4 The urgency-gating mechanism*

352 A decreasing accuracy criterion can be implemented in mathematical models through an  
353 increasing gain of neural activity and a fixed firing threshold, as supported by recent  
354 computational and neurophysiological results (see 4.1 in Discussion). I thus used the urgency-  
355 gating model (41) to find, separately for each block and each session, the slope and intercept of

356 urgency that produced the best estimate of the SumLogLR curve (in the least-mean-squared error  
357 sense) with data combined across trials. The best fitting parameters are shown in Figure 3C,D,  
358 along with the mean and standard deviation of the parameters estimated based on a bootstrap  
359 procedure. Although the simple assumption of a rectified linear urgency signal only  
360 approximately captured the shape of the SumLogLR curves for data collected in sessions #1, the  
361 quality of fit was remarkably good for sessions #2 data, as shown in Figure 3C (left). For these  
362 sessions, the urgency functions that best reproduce the data show a similar pattern: In the slow  
363 block, the urgency has a lower y-intercept but a higher slope than in the fast block. Consequently,  
364 although the urgency signal is initially lower in the slow block, the two functions eventually  
365 converge ~2100ms after the start of token movements. This makes sense because the difference  
366 in the amount of time potentially saved in the fast blocks versus slow blocks decreases as the  
367 number of remaining tokens decreases. Thus, later in the trial there is less of an advantage to  
368 behave differently in the two blocks. This results remarkably matches what my colleagues and I  
369 previously observed in highly trained monkeys performing the same task (25).

### 370 *3.5 Rate of correct responses and expected time to complete the task*

371 In this task, spending time to collect more sensory evidence usually improves accuracy. This is  
372 important because subjects had to make 320 correct decisions to complete each of the two  
373 sessions. However, as time is passing, the loss in terms of *rate* of correct choices may exceed the  
374 benefit of potentially gaining accuracy (see equation 2 in Methods), especially in a dynamic  
375 environment in which one does not know whether better evidence will ever come. The urgency  
376 signal has been hypothesized as an efficient way to prevent spending too much time on uncertain  
377 choices, resulting in reward rate optimization (12–17), what ultimately matters the most for  
378 subjects engaged in multiple trials decision-making tasks (10,11). How did adjustments of the

379 urgency signal affect subjects' rate of reward (i.e. their expected time to complete the task)?  
380 Figure 4A shows that on average, fast blocks were completed faster than slow blocks (17min30s  
381 versus 21min in sessions #1; 17min30s versus 20min12s in sessions #2; WMW tests,  $p < 0.0001$   
382 for the two comparisons). Interestingly, the main difference between the two sessions concerns  
383 the slow block, with a reduction of the expected time to complete the task based on choice  
384 behavior between sessions. This result, initially surprising with respect to the observation that  
385 decision durations in slow blocks increased in sessions #2 compared to sessions #1, means that  
386 subjects took longer to decide, leading to higher success probabilities, thus less errors and finally  
387 less required trials to complete the task. This result is also consistent with the modelling results  
388 where the urgency shape was mainly adjusted between sessions in the slow block of trials (Fig.  
389 3D). Together, these results suggest that subjects adjusted their decision policy (in terms of  
390 decision duration and success probability) by shaping their urgency signal between blocks and  
391 sessions in order to ultimately optimize their rate of reward. This is further supported by data  
392 from the two subjects who performed six and seven sessions in the tokens task. In these two  
393 subjects, decision durations and success probabilities evolved and differed between blocks  
394 through sessions, resulting in a constant and block-independent decrease of the expected time to  
395 complete the task (Fig. 4B).

### 396 *3.6 Reaching behavior*

397 Did decision policy affect reach movement kinematics? Figure 5A shows distributions of one  
398 subject's decision durations in each of the two block conditions and in each of the two sessions.  
399 This subject made slower choices in the slow block compared to the fast block but only in session  
400 #2. Figure 5B shows the velocity profiles of her reaching movements in the same conditions, for  
401 the two potential start-target distances (see 2.3 in Materials and Methods). Regardless of that

402 distance, velocity of the reaching movements executed to report the choices were faster in the fast  
403 block compared to the slow block, but only in session #2. At the population level, I found that  
404 peak velocity of reaching movements was significantly higher in fast block than in slow block in  
405 8 out of 17 subjects in sessions #1 and in 9 out of 17 subjects in sessions #2 (Fig. 6A top panels,  
406 WMW test,  $p < 0.05$ ). When velocity was divided by amplitude to get an estimation of movement  
407 vigor, I found that vigor was higher in fast block than in slow block in 12 out of 17 subjects in  
408 sessions #1 and in 14 out of 17 subjects in sessions #2 (Fig. 6A middle panels, WMW test,  
409  $p < 0.05$ ). When considering movement duration, which might be the metric that matters the most  
410 for subjects trying to optimize their rate of reward, I found that movements were overall shorter  
411 in fast blocks compared to slow blocks, especially in sessions #2 (9/17, WMW test,  $p < 0.05$ , Fig  
412 6A bottom panels). To assess whether a relationship between the difference of decision durations  
413 between blocks and the corresponding movement metrics exists (as suggested by data depicted on  
414 Fig. 5), I computed a Pearson correlation coefficient between the difference of decision durations  
415 between blocks and the difference of movement metrics (peak velocity, vigor and duration)  
416 between blocks across subjects (Fig. 6B). Results show no significant correlation in sessions #1,  
417 although a trend is visible for movement duration (Pearson  $r = 0.46$ ,  $p = 0.06$ ). By contrast, a  
418 significant correlation between the adjustments of decision durations and movement peak  
419 velocity ( $r = -0.54$ ,  $p = 0.03$ ) and duration ( $r = 0.61$ ,  $p = 0.009$ ) has been found in sessions #2  
420 data. In both cases, it is worth noting that the linear model predicts a  $\sim 0$  difference of kinematics  
421 between blocks when the difference of decision durations is close to 0 too. A trend, but not  
422 significant ( $r = -0.42$ ,  $p = 0.09$ ), has been found for movement vigor. To summarize, I found that  
423 the largest the difference of decision duration between the blocks of sessions #2, the largest the  
424 difference of movement kinematics between those two same blocks.

425 This observation suggests that decision urgency, the signal that determines subjects' deliberation  
426 duration, also affects movement properties. If so, we should also observe the signature of urgency  
427 on movement kinematics within blocks of trials, when data are sorted as a function of decision  
428 duration. More precisely, if movement kinematics is fully determined by decision urgency, we  
429 should observe (based on the urgency shapes estimated in Fig. 3D) (1) an overall increase  
430 (decrease) of velocity and vigor (duration) as a function of decision duration regardless of the  
431 block condition, (2) higher (lower) velocity and vigor (duration) in fast block compared to slow  
432 block, and (3) largest differences between blocks in all metrics for the longest decisions in  
433 sessions #1 but largest differences between blocks for the shorter decisions in sessions #2. These  
434 three predictions are validated for the effect of decision duration on reaching velocity during  
435 sessions #1 (Fig. 7, top left panel): peak velocities increased with decision duration (ANCOVA,  
436 peak velocity, time effect:  $F_{(1,345)} = 7.65$ ,  $p = 0.006$ ), velocities were higher in fast blocks  
437 compared to slow blocks (block effect:  $F_{(1,345)} = 9.49$ ,  $p = 0.002$ ) and this difference tended to be  
438 larger for long decisions compared to short decisions, despite the interaction between time and  
439 block was not significant (time x block interaction:  $F_{(1,345)} = 1.8$ ,  $p = 0.18$ ). In sessions #2 (Fig. 7,  
440 top right panel), the first two predictions are also validated, with an increase of reaching peak  
441 velocities as decision durations increased (peak velocity, time effect:  $F_{(1,332)} = 5.89$ ,  $p = 0.01$ ) and  
442 higher velocities in fast blocks compared to slow blocks (peak velocity, time effect:  $F_{(1,332)} =$   
443  $7.96$ ,  $p = 0.005$ ). However, there was no significant interaction between time and block on peak  
444 velocities (peak velocity, time x block interaction:  $F_{(1,345)} = 0.26$ ,  $p = 0.611$ ), indicating that the  
445 largest difference of urgency level between the two blocks estimated at the beginning of the trial  
446 did not fully translate on reaching peak velocities. The same effects were observed when vigor of  
447 movement was analyzed instead of peak velocity (Fig. 7, middle panels). When movement  
448 duration was considered, the same effects were observed regardless of the two sessions:

449 movement durations significantly decreased as decision durations increased (movement duration,  
450 time effect:  $F_{(1,345)} = 31$ ,  $p < 0.001$  in sessions #1;  $F_{(1,332)} = 21$ ,  $p < 0.001$  in sessions #2) and  
451 reaching durations were longer in slow block compared to fast blocks (time effect:  $F_{(1,345)} = 8.3$ ,  $p$   
452  $= 0.004$  in sessions #1;  $F_{(1,332)} = 7.3$ ,  $p = 0.007$  in sessions #2). While data seem to indicate that  
453 difference between blocks was larger for short decisions compared to slow decisions (in both  
454 sessions #1 and #2) there was no significant interactions between blocks and decision time on  
455 movement duration. Taken together, the above results suggest that decision urgency strongly, but  
456 not fully, determine reaching movement properties in the token task.

### 457 *3.7 Oculomotor behavior*

458 In the tokens task, eye movements were unconstrained and had no influence on reward rate.  
459 Nevertheless, if the urgency signal is a global, unspecific arousal signal as suggested in previous  
460 studies (42–44), then that signal may also invigorate the saccades made during the course of the  
461 decision process (25). To test this prediction, I focused my analysis on saccades made between  
462 the two lateral circles during the deliberation period. For technical reasons, data from 13 out of  
463 17 subjects have been included in this analysis. This dataset consists of 1452 trials and 2930  
464 saccades in the slow blocks, 1339 trials and 2600 saccades in the fast blocks. When all saccades  
465 made before the decision were grouped as a function of their latency with respect to the start of  
466 token movements, results showed a highly significant increase of peak velocity, amplitude and  
467 duration over the time course of trials, in both blocks and both sessions (Fig. 8, ANCOVAs,  
468 effect of time on saccade peak velocity, amplitude and duration,  $p < 0.01$ ). For instance, the  
469 average peak velocity of saccades increased from 500 deg/s around deliberation onset to more  
470 than 600 deg/s after 2s of deliberation. However, in sharp contrast with what has been observed  
471 on reaching movements, there was no significant difference of saccade velocity, amplitude or

472 duration between slow and fast blocks of trials, as one would have predicted if the urgency signal  
473 strongly influences saccade properties. Only significant interactions between block and time for  
474 duration and amplitude of saccades made in sessions #2 were found (duration, time x block  
475 interaction:  $F_{(1,225)} = 5.6$ ,  $p = 0.02$ ; amplitude, time x block interaction:  $F_{(1,225)} = 6.6$ ,  $p = 0.01$ ),  
476 with the increase of saccade duration and amplitude with deliberation time only occurring in the  
477 fast block.

#### 478 **4. DISCUSSION**

479 In the present study, I tested the hypothesis that naïve human subjects faced with a probabilistic,  
480 changing evidence decision-making task trade speed against accuracy to maximize their rate of  
481 reward by adjusting an urgency signal, and that this urgency signal also influences the way  
482 subjects overtly report their decisions via arm movements. The results support the hypothesis,  
483 showing a context-dependent correlation between two phenomena traditionally considered  
484 separate: the accuracy criterion for decisions and the duration of movements used to report them.  
485 This observation is consistent with what has been previously demonstrated in intensely trained  
486 macaque monkeys in the same experimental design: urgency, possibly computed in the basal  
487 ganglia (27–29), not only controls decision-making timing, but also influences the speed of the  
488 following motor commands, whether movements directly influence reward rate or not (25,26).

##### 489 *4.1 Urgency-based decision-making*

490 Traditional models of decision-making assume a simple mechanism in which sensory information  
491 is temporally integrated until a static choice threshold is crossed (45,46). Importantly, all these  
492 models assume that the speed-accuracy trade-off is controlled by the distance between the initial  
493 activity of the integrators (i.e. the baseline) and the response threshold: lowering the threshold in  
494 some blocks of trials leads to faster responses at the expense of an increase in error rate in these

495 blocks. More recently, computational work has included an “urgency” component in the decision  
496 process in order to explain data in ecological scenarios and to propose a more satisfying  
497 mechanistic explanation of how decisions between actions are implemented in the brain (12,13).  
498 Urgency is usually considered as an evidence-independent component of neural decision signal  
499 activity that expedites choice commitment under uncertainty (12,13,47). As a consequence,  
500 urgency-based decision models have been shown to better account for reward rate maximization,  
501 what ultimately matters the most for subjects engaged in goal-oriented behavior (11), than classic  
502 accumulation to static threshold models (12–17). Such urgency signal can be (roughly  
503 equivalently) accommodated in mathematical models either as a dynamic adjustment to the  
504 quantity of evidence required to trigger commitment (i.e. a collapsing decision threshold (39)) or,  
505 more consistently with neurophysiological observations (13,18,48), as a rising signal that is  
506 combined to sensory evidence until a fixed decision threshold is crossed (e.g. the urgency-gating  
507 model (41)), altogether forming time-variant models of decision-making. The present work  
508 replicates the observation that a context-dependent urgency-based decision policy is adopted by  
509 human subjects facing changing conditions, a result first described in the original study that used  
510 the tokens task (41) and later in variants of this task (15,49,50). It also provides several important  
511 additional observations: (1) the decision policy within and between speed-accuracy trade-off  
512 conditions is fine-tuned through practice, coinciding with an increase of the subjects’ rate of  
513 reward and (2) the decision policy strongly influences the way subjects report their choices via  
514 reaching movements. These two observations and their implications are discussed in the  
515 following sections.

#### 516 *4.2 Human versus monkey behavior*



517 A significant amount of support for time-variant models comes from the neurophysiological  
518 literature exploring decision-making strategies in non-human primates (13,18,19,51), raising the  
519 possibility that urgency-based decision policy is specific to “impatient” species, such as monkeys  
520 (35,39). For instance, Hawkins and colleagues found that static threshold models (assuming no  
521 urgency) make a better description of some human data sets than time-variant models whereas  
522 the urgency-gating model is more accurate in predicting monkeys’ behavior (39). It is indeed  
523 possible that naive human subjects instinctively prioritize precision over all other objectives  
524 (perhaps because of pride) and thus set a low level of urgency to guarantee high percentages of  
525 correct responses, even at a high cost of time. By contrast, monkeys, as impulsive animals in  
526 nature, would typically make very rapid decisions, betting more on the overall success (and  
527 reward) rate instead of performance per se (52).

528 The present data do not support this hypothesis, as most subjects adopted an urgency-based  
529 decision policy (i.e. a dropping accuracy criterion) that was adjusted depending on the reward  
530 rate context of the task irrespective of the session they performed (Fig. 3). More investigations  
531 are needed in order to assess whether or not these conclusions are generalizable to other studies,  
532 as it is likely that decision-making mechanisms are at least partially task dependent. However,  
533 they are consistent with numerous recent studies (but see (37,38)) that have demonstrated that  
534 naïve human decision-makers decrease their accuracy criterion as time is passing within a trial  
535 when making successive decisions between actions, whether these decisions are guided by  
536 sensory or value cues (15–17,40–44,53–56).

#### 537 *4.3 Effect of practice on decision policy*

538 Logically, the effect of practice history has been put forward as another explanation for differences  
539 in decision policies within and across animal species (11,36,39,52). A large amount of practice

540 necessarily shaping subjects' behavior, it would allow them (usually monkeys) to explore more  
541 strategies than subjects (usually humans) faced with only a few experimental sessions. However,  
542 the present results show that most of the subjects made urgency-based decisions as soon as they  
543 performed their first experimental session (Fig. 3A). Such urgency-native behavior is in agreement  
544 with a recent study in which time-variant models provided better fits than time-invariant ones to  
545 data from two classic response time paradigms, regardless of subjects' practice load (40).  
546 Nevertheless, the present data also show some degree of experience-dependent adjustment of  
547 urgency level: first, subjects lowered their baseline urgency level in the slow block of session #2  
548 compared to session #1 (Figs 2D and 3D). This is interesting because it means that naïve subjects  
549 started to perform the task in a rather "impulsive" mode and then only became more conservative  
550 with practice. Remarkably, after only one session, the shapes of the subject's urgency functions  
551 looked on average very similar to the ones of two highly trained monkeys in the exact same task  
552 (compare Fig. 3D and Fig. 3B in 25): difference of urgency between blocks was larger for short  
553 decisions compared to long decisions, which is the good strategy to adopt in this task where the  
554 difference in the amount of time potentially saved between blocks diminishes as tokens are jumping  
555 in a trial. Second, in the two subjects tested six and seven times, decision policy (decision duration  
556 and success probability) constantly evolved through sessions, possibly reflecting the fine-tuning of  
557 the block-dependent urgency functions permitting the minimization of the time necessary to  
558 complete each session (i.e. to maximize the rate of reward, Fig. 4B). In a recent study, Evans and  
559 Hawkins (36) addressed a similar question with respect to the decision-making process, looking at  
560 whether human subjects performing a motion discrimination task were more likely to adopt  
561 collapsing thresholds after practice and/or feedback delays. Interestingly, they found that  
562 participants adopted fixed thresholds before practice and without feedback delays, but that they  
563 behaved according to an urgency-based mechanism from the first session if the decision feedback

564 was slightly delayed in time, mirroring a response deadline context. Crucially, in this feedback  
565 delayed condition, steepness of collapsing thresholds almost continuously increased through the  
566 successive sessions performed by the subjects.

#### 567 *4.4 An unified mechanism of control during decision and action?*

568 The slight evolution of subjects' decision strategy between the two sessions provides us with a  
569 good opportunity to investigate the strength of that policy effect on movement kinematics.  
570 Indeed, a simple way to explain the correlation between decision criterion and movement  
571 kinematics in the tokens task is to suppose that the vigor of movements is in part influenced by  
572 the level of the urgency signal at decision time (30,31). But how strong is this influence and why  
573 would that common regulation exist? On one hand, the effect of block on the kinematics of  
574 movements executed to report these decisions was more pronounced in session #2 compared to  
575 session#1 (Fig. 6A). Because the difference of urgency level between blocks was larger in  
576 session #2 compared to session #1 as well, one may propose that the urgency signal at the time of  
577 commitment strongly determines kinematics of the ensuing movements. But on the other hand,  
578 the non-significant correlation between decision duration and movement parameters in sessions  
579 #1 forces us to tone this proposal down. Moreover, when the effect of decision duration on  
580 movement properties is investigated within blocks, modulations of movement speed, vigor or  
581 duration appear similar irrespective of the session (Fig. 7). If movement kinematics was directly  
582 under the control of decision urgency, one would have observed session-dependent differences of  
583 movements metrics between and within blocks, with modulations resembling the shape of the  
584 urgency functions estimated based on subjects' decision behavior. Taken together, these  
585 observations suggest that although decision urgency strongly and innately influences movement  
586 kinematics, decision-making and movement control are not strictly unified processes (57).

587 A link between deliberation and movement kinematics makes perfect sense in the context of  
588 reward rate maximization. In the tokens task, the tokens remaining in the central circle start to  
589 accelerate only after the cursor enters the chosen target. As a consequence, the longer the  
590 movement, the longer the period separating its completion from reward. Thus, because reward  
591 rate is influenced by the time spent executing the movement, urgency might exert a compensatory  
592 influence on handling time, such that the cost of investing additional time in deliberation will be  
593 partially offset by a decrease in the duration of the movements used to report the choice. In  
594 agreement with this hypothesis, it has been shown that human movements are parameterized  
595 following economical rules: expectation of reward increases speed of movements, whereas  
596 expectation of effort decreases this speed (20–24). This possibility would also explain why a  
597 motor system that does not directly impact the rate of reward in this task (i.e. the oculomotor  
598 system) does not appear as strongly modulated by urgency as one directly involved in reward rate  
599 maximization (i.e. the reaching motor system, Figs. 7 and 8).

#### 600 *4.5 A neurophysiological mechanism to optimize the rate of reward*

601 The neural mechanisms that contribute to the optimization of the reward rate are poorly  
602 understood. Several arguments point toward the sensorimotor territory of the basal ganglia (BG)  
603 as a brain region that could compute a global signal capable of determining both decision and  
604 movements speed in order to optimize this rate. First, the BG integrate rich sensory and motor  
605 information from the neocortex with reward-related dopaminergic signals. This information is  
606 further processed throughout the BG nuclei where a dramatic reduction in neuron number occurs,  
607 thereby contributing to the formation of a low-dimensional integrated signal that could efficiently  
608 modulate neuronal activity in the entire neocortex through recurrent dynamics (29,58). Second,  
609 electrophysiological recordings in the sensorimotor regions of the globus pallidus and dorsal

610 striatum (output and input of the BG, respectively) of behaving non-human primates and rodents  
611 are consistent with the hypothesis that the BG motivate voluntary behavior, including the urgency  
612 to decide (29,59) and the vigor of movements (60–62). Last, a reduction in goal-directed  
613 movement speed is common to non-human primates with BG output inactivation, human subjects  
614 with lesions in their BG and patients suffering from Parkinson's Disease (33,34,63). In the latter  
615 case, slowness of cognition, including decision-making, is often reported (64).

#### 616 *4.6 A « trait-like » view of urgency*

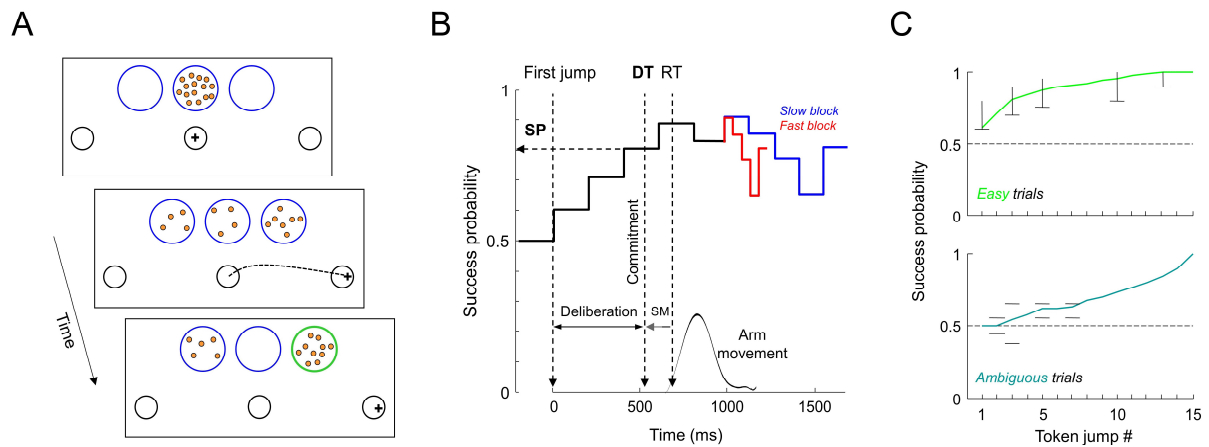
617 A limitation of the present study, as often in the study of primate cognition and behavior, relates  
618 to the fact that subjects might have employed various strategies to solve the task depending on  
619 their personality. The large inter-subject variability observed in terms of decision duration  
620 supports this possibility (Fig. 2C-2D). Strikingly, the average decision duration ranged from  
621 ~700ms to about 1600ms depending on subjects, despite the fact that these participants faced the  
622 same trials under identical conditions. This strongly suggest some “trait” levels of decision  
623 urgency, consistently with what has been found during movement behavior: some subjects  
624 perform movements up to four times faster than others (30,57,65). Thus, even though such  
625 variability might at first sight blur any conclusive statement about a “standard” decision  
626 mechanism employed by subjects to solve the tokens task, it could instead provide fundamental  
627 insights regarding subjects’ personality traits. My colleagues and I indeed recently proposed that  
628 decision-makers might control diverse behavioral outputs based on a urgency-mechanism whose  
629 “default” setting is proper to each individual but varies across them (32).

## 630 **5. CONCLUSION**

631 Taken together, the present results suggest that urgency might provide the mechanistic link for  
632 establishing a strong (but not perfect) control of decision timing and action vigor in “non-expert”

633 human subjects in order to optimize the rate of reward. Because it has been proposed that urgency  
634 controls the timing of both decisions and movements through projections from the basal ganglia  
635 to sensorimotor regions (27–29,42,44,61), it might also influence many other aspects of  
636 motivated behavior through projections to other cortical regions, including prefrontal and limbic  
637 areas. Urgency could thereby accounts for inter-individual differences in a variety of specific  
638 traits, and possibly even some symptoms of neurological disorders (32–34).  
639

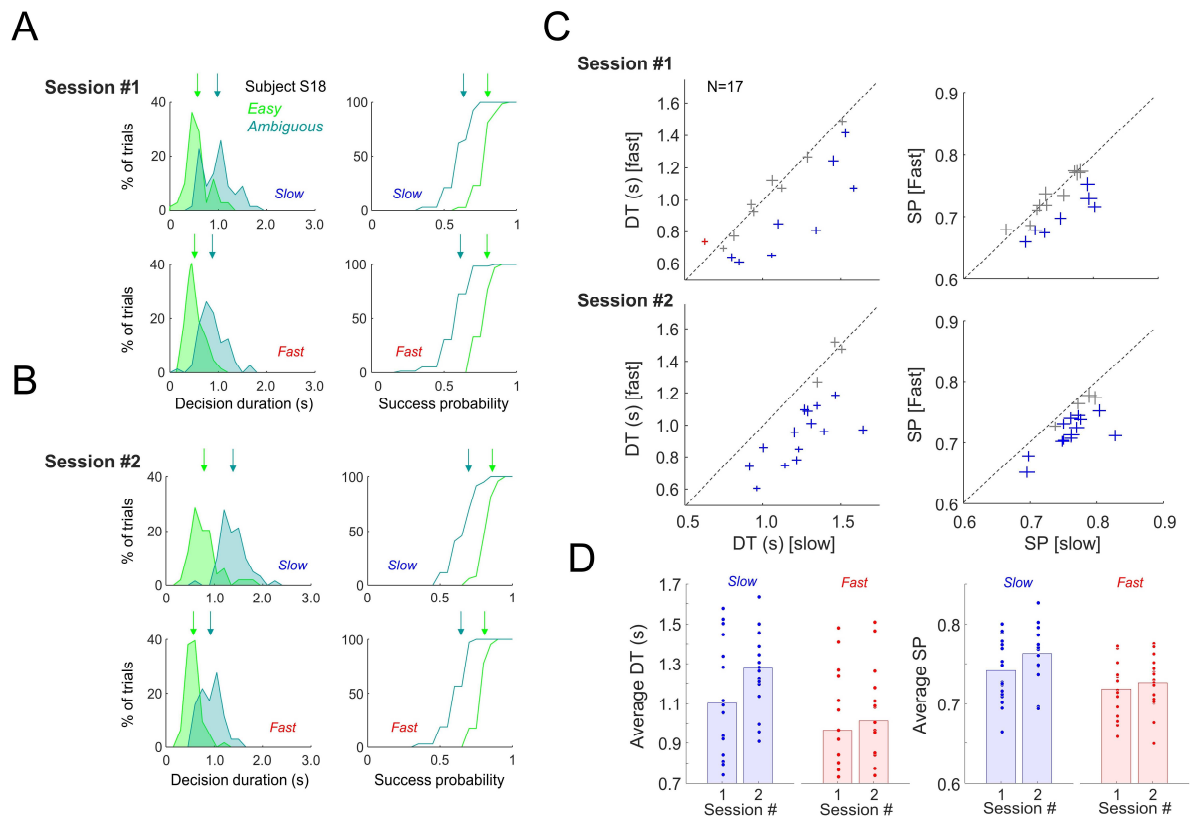
640 **6. FIGURE CAPTIONS**



641

642 *Figure 1 – The tokens task*

643 **A.** Time course of a trial in the tokens task. Blue circles illustrate the decision stimuli. Tokens  
644 successively jump from the central circle to one of the two lateral circles. Black circles show the  
645 movement stimuli. Subjects move a lever (cross) from a central “start” circle to one of the two  
646 lateral targets, depending on their choice. Reaching targets size and distance could vary in blocks  
647 of trials (effects of target features are not investigated in the present paper, see 2.3 in Methods) **B.**  
648 Temporal profile of success probability in an example trial. During deliberation, response  
649 preparation and execution, tokens jump every 200ms. The estimated time of the decision (DT) is  
650 computed by subtracting the subject’s mean sensory-motor delay (SM) estimated in the delayed  
651 reach task from movement onset time (RT), allowing computation of the success probability (SP)  
652 at that moment. After movement completion, the remaining tokens jump more quickly in their  
653 assigned lateral circles, either every 150ms (“slow” block, blue) or 20ms (“fast” block, red). For  
654 clarity reasons, only 10 out of 15 jumps are illustrated on this trial SP profile. **C.** Average success  
655 probability profiles of easy (green) and ambiguous (blue-green) trials. Criteria (black marks)  
656 were used to define these special trials interspersed among fully random trials. For instance, a  
657 trial is classified as “easy” if  $SP > 0.6$  after the first token jump (i.e. if the first token jumps into  
658 the correct circle),  $SP > 0.7$  after 3 jumps, etc. A trial is classified as ambiguous is  $SP = 0.5$  after  
659 the second jump,  $SP$  between 0.38 and 0.65 after 3 jumps,  $SP$  between 0.55 and 0.65 after 5  
660 jumps, etc.



661

662 *Figure 2 – Effect of trial difficulty and SAT context on decision policy*

663 **A.** Distribution of subject S18 decision duration (left panels) and success probability (right  
 664 panels) during easy (green) and ambiguous (blue-green) trials performed in either the slow (top  
 665 panels) or fast (bottom panels) blocks of the tokens task during her first experimental session.

666 Colored arrows illustrate the means of the distributions. **B.** Same as *A* for subject S18 data

667 collected in session #2. **C.** Average decision times (left panels) and success probabilities (right

668 panels) of each subject during slow (x-axis) and fast (y-axis) blocks performed in the first (top

669 panels) and the second (bottom panels) session. Blue pluses indicate the mean and SE for

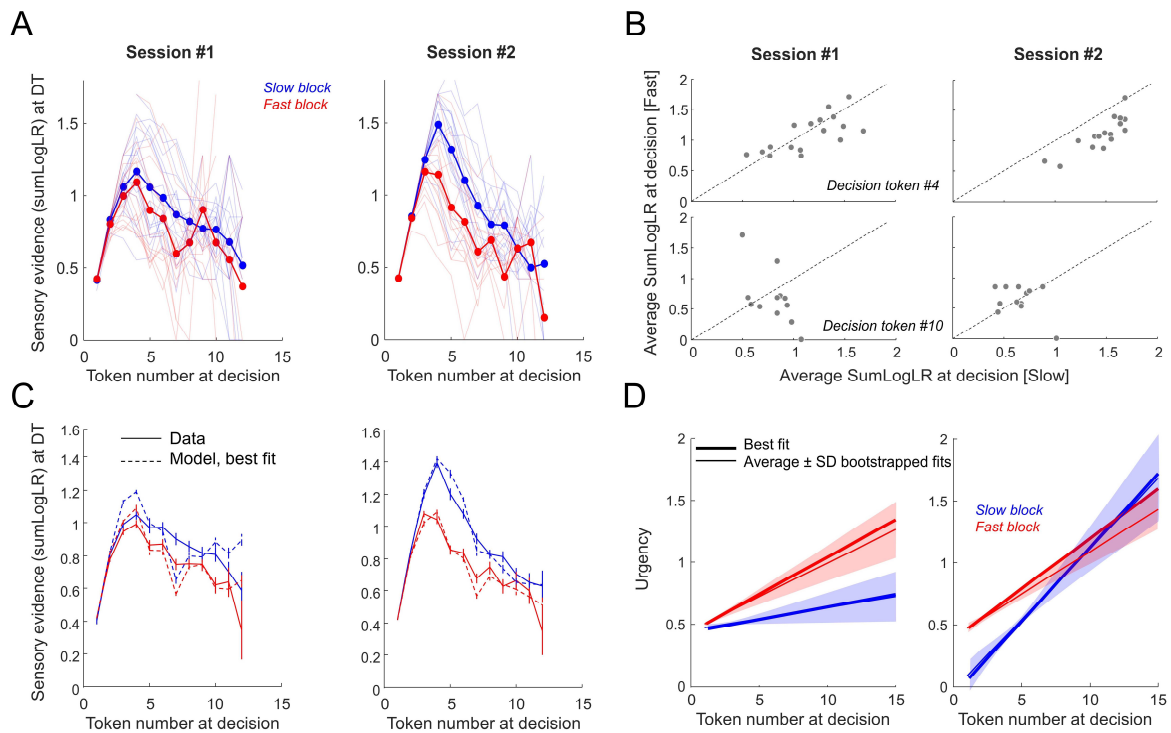
670 subjects for whom the difference was significant (WMW test,  $p < 0.05$ ). **D.** Average decision times

671 (left panel) and success probabilities (right panel) across the population as a function of the

672 session number and the block condition. Dots illustrate individual data.

673

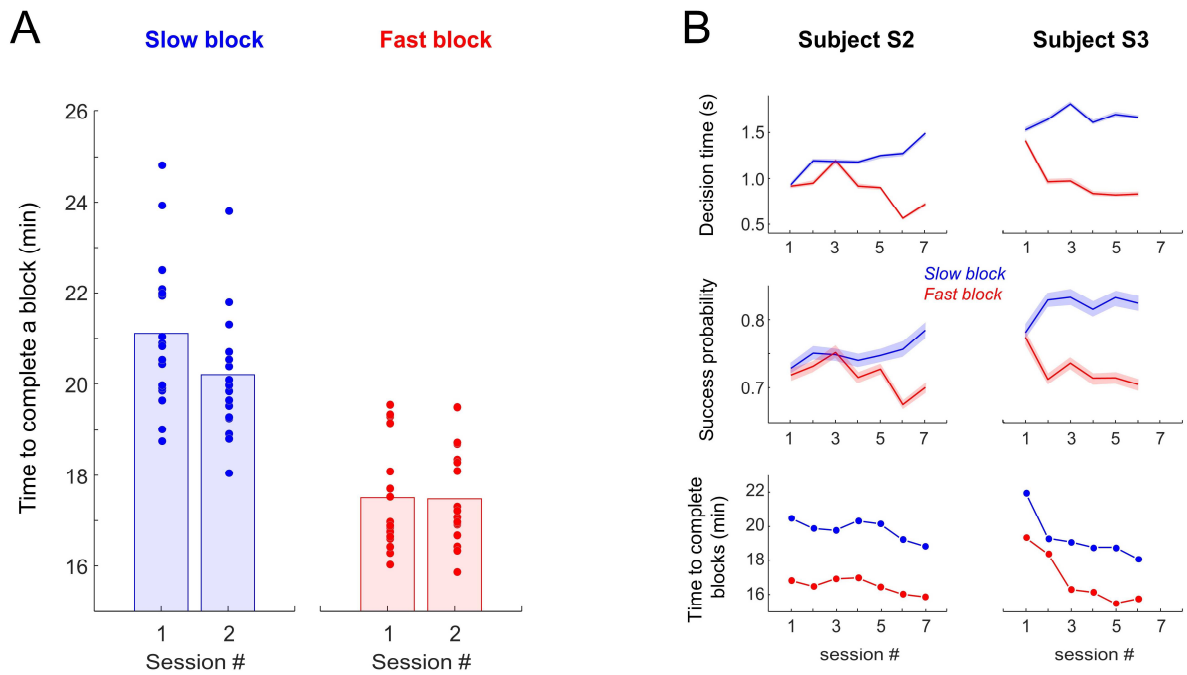




674

675 *Figure 3 – Urgency-gating mechanism*

676 **A.** Average estimate of subjects' accuracy criterion (calculated as the SumLogLR) at decision  
 677 time as a function of decision duration (in 200ms bins) during slow (blue) and fast (red) blocks in  
 678 sessions #1 (left panel) and #2 (right panels). Faded lines illustrate individual data. **B.** Average  
 679 SumlogLR at decision time of each subject during slow (x-axis) and fast (y-axis) blocks either  
 680 after 4 (top panels) or 10 (bottom panels) token jumps, during sessions #1 (left panels) and  
 681 sessions #2 (right panels). **C.** Average  $\pm$  SE SumLogLR computed across all trials compared,  
 682 separately for each block type, with the SumLogLR computed using the best-fit urgency-gating  
 683 model (dotted line  $\pm$  SE) with a simple linearly increasing urgency function, shown in D. Left  
 684 panels show data collected in sessions #1, right panels illustrate data collected in sessions #2. **D.**  
 685 Urgency functions estimated based on the best fit of the urgency-gating model (bold lines) and  
 686 mean  $\pm$  SD urgency functions estimated based on a bootstrap procedure (thin lines and shaded  
 687 areas) for each block type (blue: slow; red: fast) and each session (left: sessions #1; right:  
 688 sessions #2).



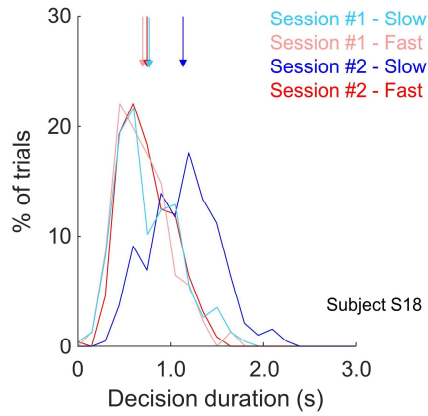
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690 *Figure 4 – Effect of SAT context and practice on reward rate*

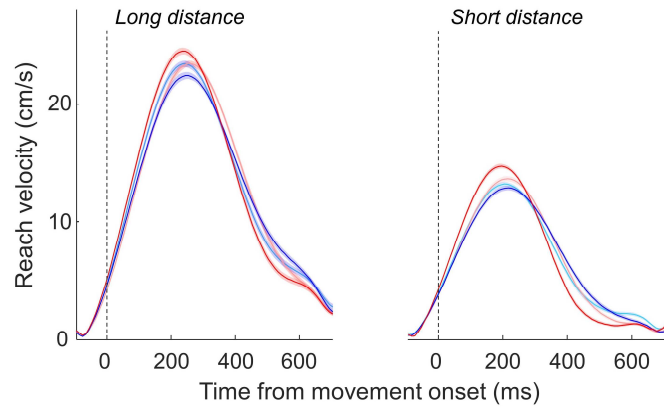
691 **A.** Average expected time to complete a block of trials across the population as a function of the  
 692 session number and the block condition. Dots illustrate individual data. **B.** Evolution of mean ( $\pm$   
 693 SE) decision durations (top panels), success probabilities (middle panels) and mean expected  
 694 time to complete a block of trials (bottom panels) during slow (blue) and fast (red) blocks as a  
 695 function of session number in subject S2 (left panels) and S3 (right panels).

696

A



B



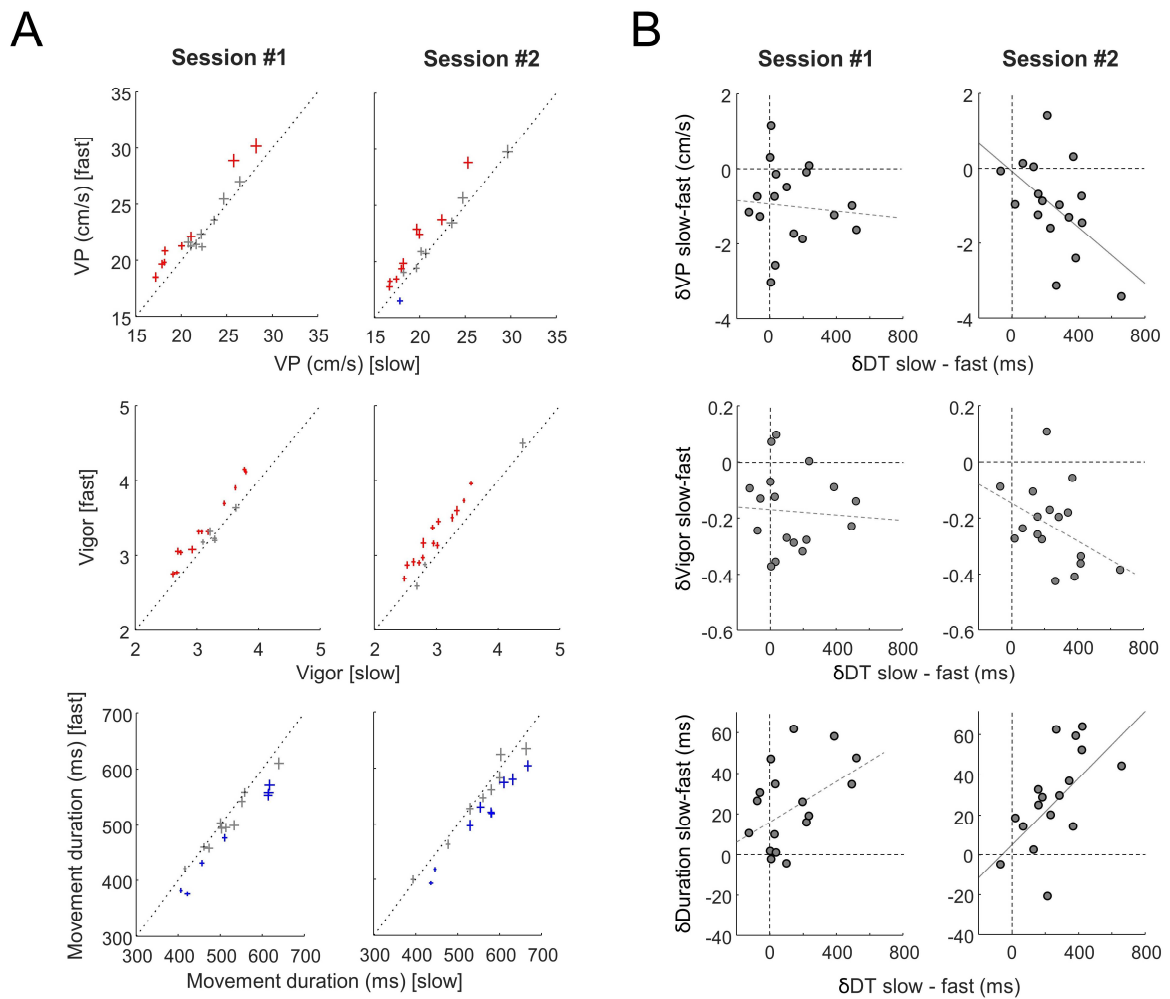
697

698 *Figure 5 – Example of movement modulation as a function of decision duration*

699 **A.** Distributions of subject S18 decision duration in the slow and fast blocks of session #1 and  
700 session #2. **B.** Reach velocity profiles of subject S18 in the slow (blue) and fast (red) blocks of  
701 session #1 (light colors) and #2 (dark colors).

702

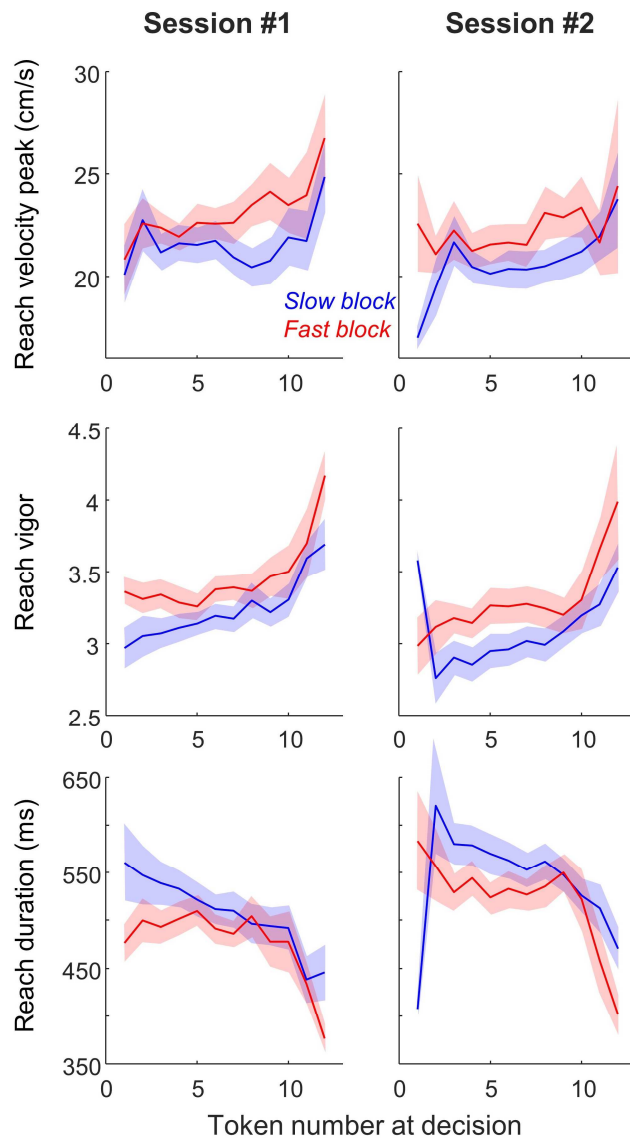
703



704

705 *Figure 6 – Correlation between decision duration and reach kinematics*

706 **A.** Average reaching movement peak velocity (top panels), vigor (middle panels) and duration  
 707 (bottom panels) of each subject during slow (x-axis) and fast (y-axis) blocks performed in the  
 708 first (left panels) and the second (right panels) session. Blue (red) pluses indicate the mean and  
 709 SE for subjects for whom data is larger (smaller) in the slow block compare to the fast block and  
 710 the difference was significant (WMW test,  $p < 0.05$ ). **B.** Difference of decision duration between  
 711 slow and fast blocks for each subject (x-axis) as a function of the difference of reaching  
 712 movement peak velocity (top panels), vigor (middle panels) or duration (bottom panels) in the  
 713 same two blocks (y-axis) performed in either the first (left panel) of the second (right panel)  
 714 session. The grey line corresponds to a linear regression through the data. The solid (dotted) grey  
 715 line illustrates a significant (non-significant) correlation between the data.



716

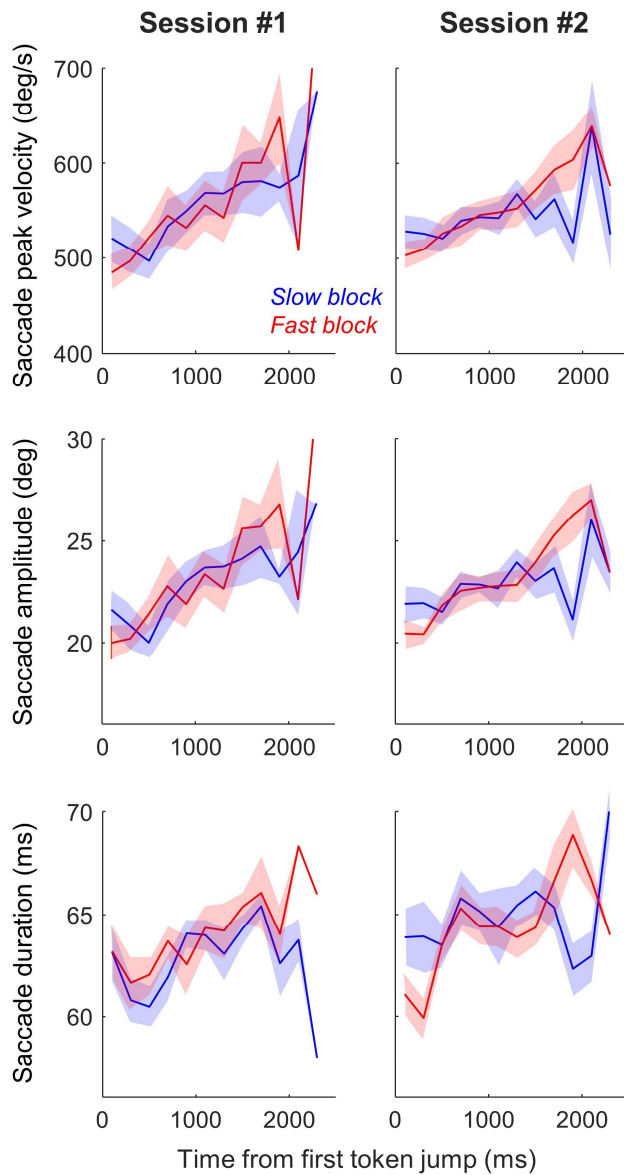
717 *Figure 7 – Effects of decision context and duration on reach kinematics*

718 Mean ( $\pm$ SE) of the peak velocity (top panels), vigor (middle panels) and duration (bottom panels)

719 of arm movement computed across subjects and binned according to decision duration in 200ms

720 bins, in the slow (blue) and fast (red) block of trials for data collected in sessions #1 (left panels)

721 and #2 (right panels).



722

723 *Figure 8 – Effects of decision context and duration on saccade kinematics*

724 Mean ( $\pm$ SE) of the peak velocity (top panels), amplitude (middle panels) and duration (bottom  
 725 panels) of saccadic eye movement computed across subjects and binned according to elapsing  
 726 time in 200ms bins, in the slow (blue) and fast (red) block of trials for data collected in sessions  
 727 #1 (left panels) and #2 (right panels).

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