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1 Humans anticipate the consequences of
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5

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29 **ABSTRACT**

30 Animals, including humans, are often faced with situations where they must decide between
31 potential actions to perform based on various sources of information, including movement
32 parameters that incur time and energy costs. Consistent with this fact, many behavioral studies
33 indicate that decisions and actions show a high level of integration during goal-directed behavior.
34 In particular, motor costs very often bias the choice process of human and non-human subjects
35 facing successive decisions between actions. However, it appears as well that depending on the
36 design in which the experiment occurs, the effect of motor costs on decisions can vary or even
37 vanish. This suggests a contextual dependence of the influence of motor costs on decision-making.
38 Moreover, it is not currently known whether or not the impact of motor costs on perceptual
39 decisions depend on the difficulty of the decision. We addressed these two important issues by
40 studying the behavior of healthy human subjects engaged in a new perceptual decision-making
41 paradigm in which the constraint level associated with the movement executed to report a choice
42 was volitionally chosen by the participants, and in which the difficulty of the perceptual decision
43 to make continuously evolved depending on their motor performance. The results indicate that the
44 level of constraint associated with a movement executed to express a perceptual decision strongly
45 impacts the duration of these decisions, with a shortening of decisions when these are expressed
46 by demanding movements. This influence appears most important when the decisions are difficult,
47 but it is also present for easy decisions. We interpret this strategy as an adaptive way to optimize
48 the participants' overall rate of success at the session level.

49 INTRODUCTION

50 Although choices are always ultimately expressed via actions, decision-making and motor control
51 are most often studied separately from each other (Gold and Shadlen, 2007; Shadmehr and
52 Krakauer, 2008; Franklin and Wolpert, 2011; Lee et al., 2012). Recent behavioral studies,
53 including ours, indicate however that decisions and actions are closely linked, sharing economic
54 principles and showing a high level of integration during goal-directed behavior (Shadmehr, 2010;
55 Gallivan et al., 2018; Carland et al., 2019; Shadmehr et al., 2019; Wispinski et al., 2020; Gordon
56 et al., 2021).

57 For instance, it has been proposed that movement selection, preparation, and execution are
58 parameterized following economical rules, varying depending on utility estimation: high valued
59 options lead to faster reaction times and movement speed, and high-perceived effort discounts an
60 option value, leading to slower reaction and longer movements (Shadmehr et al., 2010; Haith et
61 al., 2012; Choi et al., 2014; Morel et al., 2017). If the sensory information guiding the choice is
62 weak and the decision takes time, humans and monkeys shorten the duration of the movements
63 expressing this choice (Thura et al., 2014; Thura, 2020; Herz et al., 2022). If the context in which
64 the task occurs encourages fast and risky decisions, humans and monkeys report these choices with
65 faster movements compared to when the task is performed in a slow speed-accuracy context (Thura
66 et al., 2014; Thura, 2020; Herz et al., 2022; Carsten et al., 2023; Saleri and Thura, 2024).

67 Conversely, several studies have demonstrated that motor costs influence decision-making as well,
68 whether choices only rely on movement properties (Cos et al., 2011; Morel et al., 2017; Michalski
69 et al., 2020; Canaveral et al., 2024), options value (Pierrieau et al., 2021; Griebbach et al., 2022)
70 or perceptual stimuli (Burk et al., 2014; Lepora and Pezzulo, 2015; Marcos et al., 2015; Hagura et
71 al., 2017). In our lab, we have demonstrated that humans and monkeys decide faster and/or with
72 less precision in order to focus on their actions when the movement expressing a choice is
73 demanding (Reynaud et al., 2020; Saleri Lunazzi et al., 2023) or time consuming (Saleri Lunazzi
74 et al., 2021; Saleri and Thura, 2024).

75 Although these studies indicate a significant level of integration between perceptual decision-
76 making and motor control processes, with notably a significant influence of motor costs on
77 perceptual decision-making, two questions need to be addressed. First, it is unknown whether the
78 impact of the motor costs on decision-making depends on the obligation for the subjects to express

79 choices in a difficult motor condition structured in a succession of many consecutive trials. Indeed,
80 in the studies cited above (Reynaud et al., 2020; Saleri Lunazzi et al., 2021, 2023; Saleri and Thura,
81 2024), the demanding motor condition was always imposed on the subjects, in dedicated blocks
82 of trials. However, it is possible that if the subject deliberately chooses to express a choice in a
83 demanding motor condition, on a trial by trial basis, to obtain a larger reward for example, the
84 impact of these motor demands on the decision process differs. In support of such a possibility, a
85 recent result indicates for instance that the level of movement effort may not influence perceptual
86 decisions when that effort is explicitly felt and integrated by human subjects (Manzone and Welsh,
87 2023), suggesting that the results of the experiments mentioned above may be specific to how
88 motor costs are manipulated. Secondly, it is currently unknown to what extent the impact of the
89 motor control demands on decision-making depends on the difficulty of the choice to make. It is
90 for instance possible that subjects sacrifice their decisions in favor of more demanding motor
91 control only when the decision is hard but that when the decision is easy, the influence of the motor
92 context is less pronounced or even disappears.

93 We investigated these two questions by studying the behavior of healthy human subjects engaged
94 in a new perceptual decision-making paradigm in which the constraint level of the movement
95 executed to report a choice was chosen by the participants, and in which the difficulty of the
96 perceptual decision to make continuously evolved depending on their motor performance. This
97 design therefore allowed us to test the effect of motor constraints on perceptual decision-making
98 when these constraints were volitionally chosen by the subjects, and it offered at the same time the
99 possibility of testing this effect on multiple levels of decisional difficulty manipulated in a gradual
100 manner.

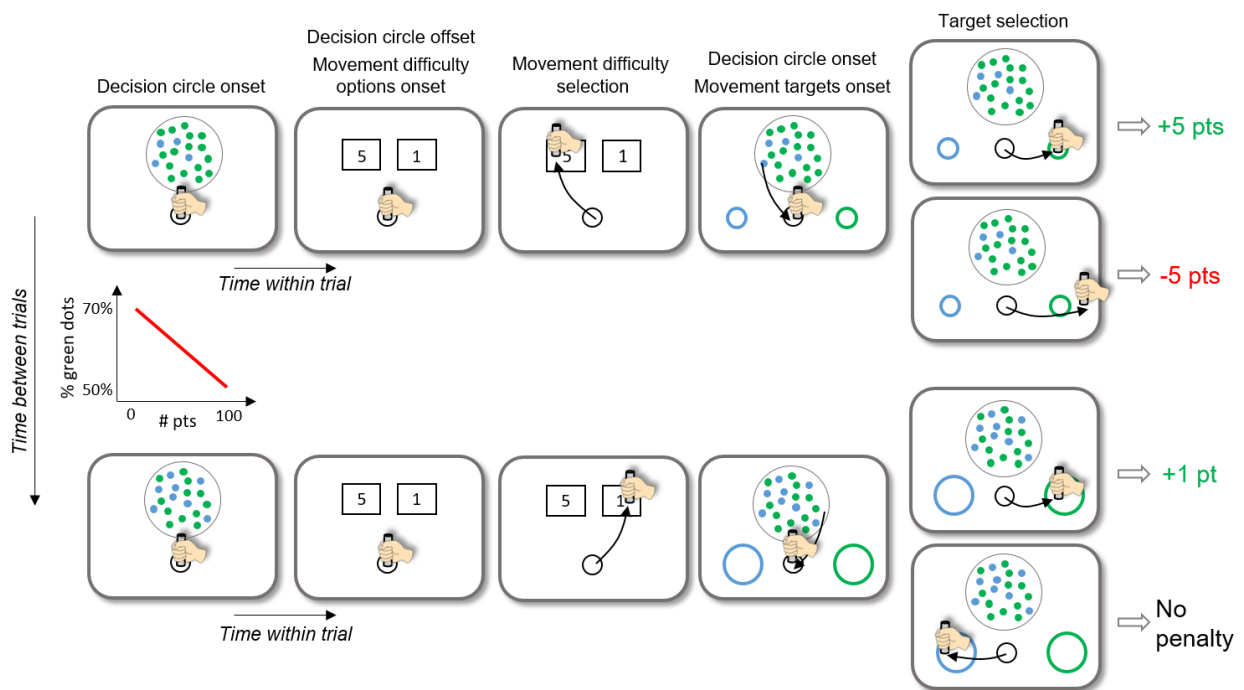
101 RESULTS

102 Thirty-two healthy human participants performed a new behavioral paradigm (Fig. 1) during a
103 single experimental session. The goal of the subjects was to accumulate a total of 200 points to
104 complete the session. To earn points, they had to choose at the beginning of each trial the constraint
105 level of the movement executed to report a perceptual decision: either a demanding arm movement,
106 in terms of motor control, potentially earning 5 points if accurately executed, or an easy movement,
107 earning only 1 point if accurately executed. After making that choice, they had to make the
108 corresponding perceptual decision and report it by executing the arm movement toward a visual

109 target. Crucially and unknown to the subjects, the coherence of the visual stimulus was linearly
 110 and inversely indexed to the number of accumulated points during the session, progressively
 111 increasing the difficulty of each perceptual decision. The points (5 or 1) that the subjects chose to
 112 engage at the beginning of each trial were lost in case of a movement error, i.e. if they failed to
 113 reach the chosen target and stay in it within the required time windows, but not in case of a wrong
 114 perceptual decision.

115 This design allowed us to assess the impact of the motor control required to express a perceptual
 116 decision on participants' decision-making performance, for decisions whose difficulty varied in
 117 small steps from an easy level to a difficult level, and when the demanding motor control condition
 118 was deliberately chosen by the subject from one trial to the next to potentially gain more points.

119



120

121 **Figure 1.** The top row illustrates the time course of a trial at the beginning of the session. Each trial starts
 122 when the subject brings with her/his dominant hand a handle and maintains it still in a start circle. The
 123 decision circle containing 100 blue and green tokens is first displayed for 300ms to inform the subject about
 124 the difficulty of the perceptual decision to make later in the trial. At this stage the dominant color among
 125 the tokens (i.e. the coherence) is not informative of the correct target to select at the end of the trial. The
 126 proportion of tokens of the dominant color is 77% on the first trial of the session. The decision circle
 127 disappears and the movement constraint options are then displayed. In this example the subject chooses “5”
 128 (by moving the handle in the rectangle surrounding the number 5), which corresponds to a demanding
 129 movement to execute, i.e. toward a small visual target ($\phi = 1.25\text{cm}$). Once selected, the subject leaves the

130 motor constraint option rectangle and comes back to the start circle. The decision circle containing the 100
131 tokens, and the blue and green movement targets then appear. The dominant color among the tokens (with
132 the same proportion as at the beginning of the trial) now determines the correct target to select. The subject
133 reports the decision by moving the handle in the target whose color corresponds to her/his choice. The
134 subject earns the amount of points she/he chose (“5” in this example) if she/he accurately reaches to the
135 correct target. She/he loses the points if she/he executes an inaccurate movement, regardless of the chosen
136 side. After the first trial, the coherence within the decision circle evolves from trial to trial, being linearly
137 and inversely indexed to the number of points accumulated during the session. As a consequence, at the
138 end of the session (bottom row), when the subject gets close to 200 points, the coherence in the visual
139 stimulus is low (proportion of tokens of the dominant color equal to 51%) and the decision difficulty is
140 high. As illustrated in this example, we assumed that in this situation, subjects would choose an easy
141 movement (the “1” rectangle), executed toward a large target ($\sigma = 3.75\text{cm}$) more frequently than at the
142 beginning of the session, when the decisional effort was low and the number of points to accumulate to
143 complete the session was high. Regardless of the movement constraint level chosen by the subject, if she/he
144 selects the wrong target (decision error) with an accurate movement, points are not deducted.

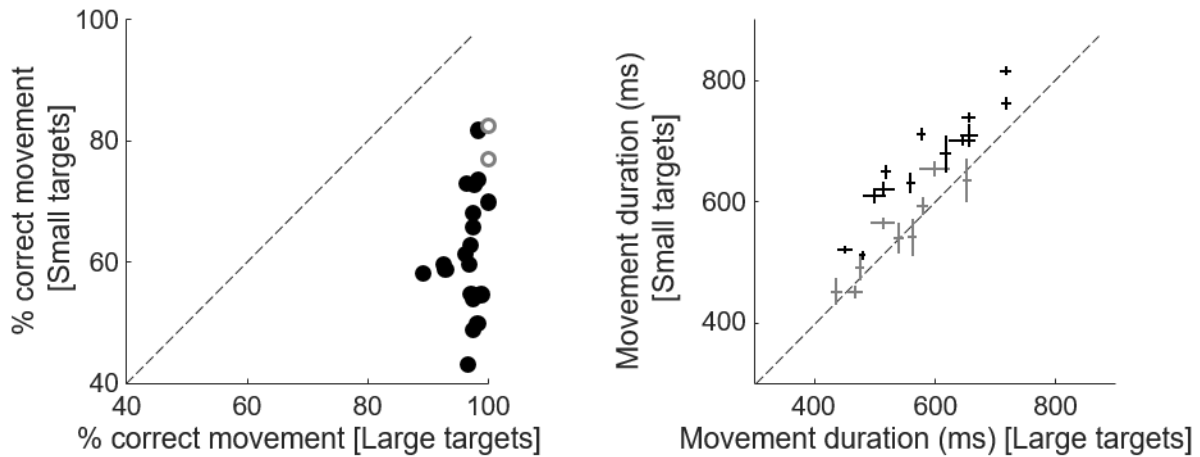
145 [General observations](#)

146 Among subjects who performed the task ($n=32$), the median number of trials to reach 200 points
147 across the population was 184, with a large variability between subjects (min = 87; max = 426; SD
148 = 84 trials). The median proportion of demanding movement choices during a session was 62%,
149 again with high variability between subjects (min: 5%; max: 100%; SD = 34%). With this design
150 we expected to observe a mixture of choices of the constraint level of the movements to be
151 performed to express the perceptual decisions, regardless of the coherence of the decision stimulus.
152 This is because the demanding movements would be chosen to gain more points, perhaps more at
153 the beginning of the session when the number of points to accumulate to complete the session is
154 high and the perceptual decisions are the easiest, while the easy movements would be chosen to
155 guarantee the obtaining of points in case of correct perceptual decisions. However, we observed
156 that out of 32 participants, 9 almost did not vary their movement difficulty choices through the
157 session (1/32 subject chose the easy option in more than 95% of the trials, 8/32 chose that option
158 in less than 5% of trials). In the following analyses, we excluded those 9 subjects who
159 systematically chose the same level of motor constraint level through their experimental session,
160 as they were likely either insensitive (for the 8 subjects who chose the difficult option in more than
161 95% of the trials) or too sensitive (for the subject who chose the easy option in more than 95% of
162 the trials) to the decisional and/or motor difficulties manipulated in the experiment.

163 [Effect of motor control demands \(i.e. target size\) on subjects’ motor behavior](#)

164 We first verified that the two constraint levels of motor control required to report perceptual
165 decisions did indeed impact the motor behavior of the remaining 23 subjects. To do this, we

166 analyzed the precision and duration of their reaching movements as a function of these two levels
 167 of constraint. As expected, we found that participants' movement accuracy was lower when they
 168 reported their perceptual decisions by moving toward the small targets compared to when they had
 169 to make a movement toward a large target (median accuracies at the population level: 60% versus
 170 97%, Chi-square test for independence on the population: $\chi^2 = 1004$, $p < 0.0001$; Chi-square tests
 171 for independence on individual subjects, 21/23 with $p < 0.05$, Fig. 2, left panel). We also observed
 172 that the majority of subjects' movements (whether accurate or not) were slower, in terms of
 173 duration, when executed toward a small target than toward a large target (Wilcoxon rank-sum tests
 174 on individual subjects, 14/23 with $p < 0.05$, Fig. 2, right panel), even if the difference of movement
 175 duration between the two motor conditions is not significant at the population level (median
 176 durations: 630ms vs. 563ms, Chi-square test for independence on the population: $\chi^2 = 1.5$, $p =$
 177 0.13). Given these results, we make the assumption in the following paragraphs that movements
 178 executed toward the small targets were more demanding, in terms of motor control, compared to
 179 movements executed toward the large targets.

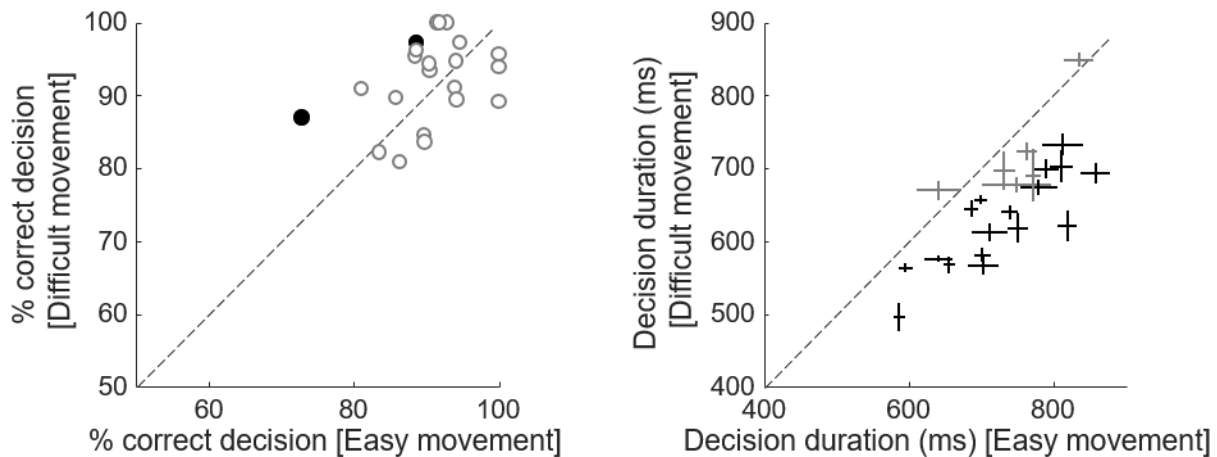


180

181 **Figure 2.** *Left panel:* Comparison of subjects' movement accuracy as a function of movement constraint
 182 level (difficult movement/small targets: ordinate; easy movement/large targets: abscissa). Circles illustrate
 183 individual subjects' data. Filled black circles highlight subjects for which the difference between conditions
 184 is statistically significant (Chi-squared test, $p < 0.05$). *Right panel:* Comparison of subjects' movement
 185 duration (whether accurate or not) as a function of movement constraint level (difficult movement/small
 186 targets: ordinate; easy movement/large targets: abscissa). Crosses illustrate individual subjects' medians \pm
 187 SE. Black crosses highlight subjects for which the difference between conditions is statistically significant
 188 (rank-sum test, $p < 0.05$).

189 [Effect of motor control demands on subjects' decision behavior](#)

190 We then analyzed the impact of this demanding level of motor control on the perceptual decisions
191 of the 23 participants. To do this, we first analyzed the accuracy and duration of their perceptual
192 decisions as a function of the motor condition in which decisions were made, regardless of the
193 difficulty of these decisions. We found at the population level that participants' perceptual decision
194 accuracy was similar whether they were reported with reaching movements executed toward small
195 or large targets (medians: 93.4% versus 90.4%, Chi-square test for independence on the
196 population: $\chi^2 = 1.9$, $p = 0.16$). Only two subjects were significantly more accurate to decide when
197 choices were expressed with difficult movements (Chi-square tests for independence on individual
198 subjects, 2/23 with $p < 0.05$, [Fig. 3, left panel](#)). By contrast, we observed that the level of motor
199 control demand strongly impacted the duration of the perceptual decisions preceding the execution
200 of movements executed to report these choices. Indeed, participants were overall faster to decide
201 (accurately or not) when the subsequent movements were demanding compared to when they were
202 easier (median durations: 657ms vs. 739ms, Chi-square test for independence on the population:
203 $\chi^2 = -3.4$, $p < 0.0001$). This effect was robust at the individual level, as the effect was significant
204 for the vast majority of subjects (Wilcoxon rank-sum tests on individual subjects, 17/23 with $p <$
205 0.05 , [Fig. 3, right panel](#)).



206

207 **Figure 3.** *Left panel:* Comparison of subjects' perceptual decision accuracy as a function of movement
208 difficulty (difficult movement/small targets: ordinate; easy movement/large targets: abscissa). Same
209 convention as in Fig. 2, left panel. *Right panel:* Comparison of subjects' perceptual decision durations
210 (correct or not) as a function of movement difficulty (difficult movement/small targets: ordinate; easy
211 movement/large targets: abscissa). Same conventions as in Fig. 2, right panel.

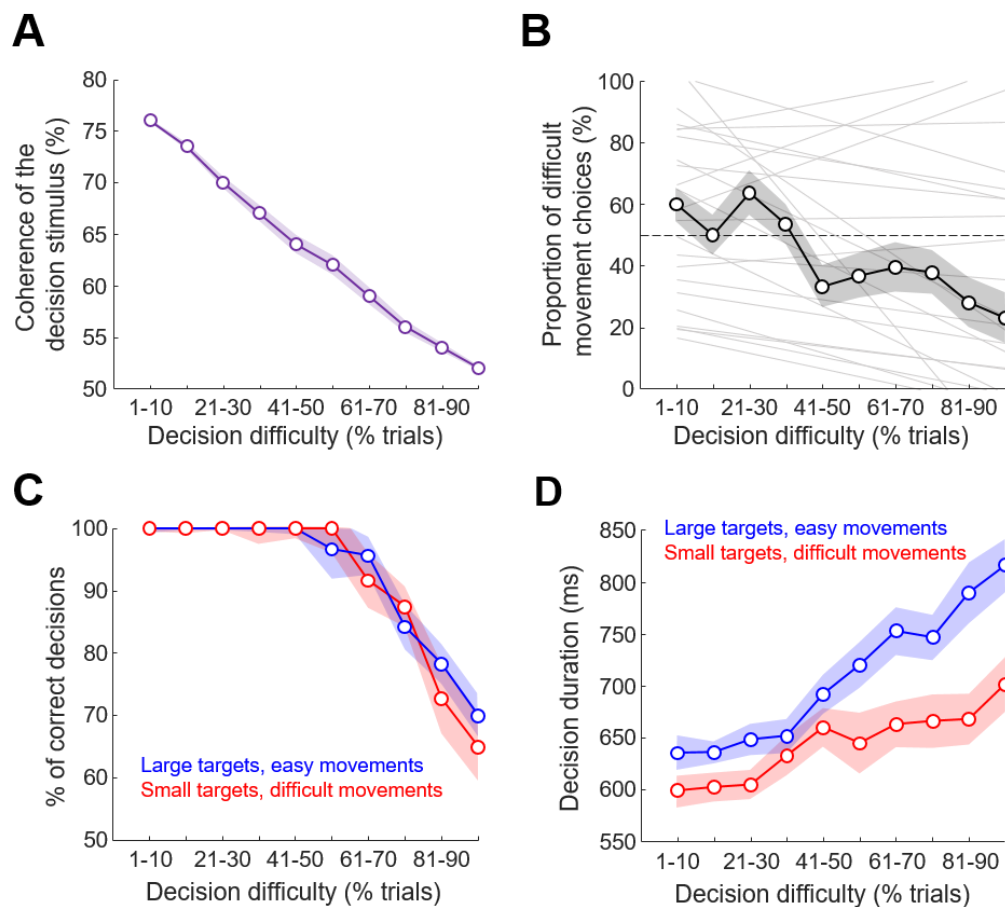
212 The above results indicate that the level of motor control required to express perceptual decisions,
213 deliberately chosen by individuals, impacts the duration of these decisions preceding the
214 movements. To answer the second question addressed in the present study, namely whether this
215 impact of motor costs on decision-making depends on the difficulty of decisions, we analyzed the
216 behavior of the subjects according to the evolution of their decisional and motor performances in
217 the task.

218 Our goal with this experimental design was to obtain trials in which subjects would volitionally
219 choose to report their perceptual decisions with easy or difficult movements, while gradually
220 increasing the difficulty of these perceptual decisions in small increments. Because the coherence
221 in the decision stimulus continuously varied from trial to trial, we normalized the number of trials
222 performed by each subject by chronologically grouping them in 10 quantiles. As shown in [figure](#)
223 [4A](#), the first 10% of trials were trials for which the coherence of the decisional stimulus was the
224 highest (because subjects' scores were the lowest) and thus perceptual decisions were the easiest;
225 Conversely, the last 10% of trials were the trials for which the coherence of the decision stimulus
226 was the lowest, and thus decisions were the most difficult.

227 We found at the population level that the proportion of difficult movement choices did not
228 significantly vary depending on the level of decision difficulty (Kruskal-Wallis test, $\chi^2 = 11.2$, $p =$
229 0.26), despite the fact that a tendency for a decrease of that proportion with the increase of decision
230 difficulty is visible ([Fig. 4B](#)). Indeed, at the individual level, we found that the evolution of the
231 perceptual decision difficulty influenced the proportion of movement difficulty choices in 17 out
232 of 23 subjects (Chi-squared tests for independence, $p < 0.05$). Among them, the vast majority
233 (13/17) overall decreased their proportion of “small targets” choices with the increase of the
234 perceptual decision difficulty ([Fig. 4B](#)).

235 We then analyzed the decision-making behavior of the participants as a function of the difficulty
236 of the perceptual decision and as a function of the level of motor control required to report these
237 choices by performing analyses of covariance (ANCOVAs). As expected, the proportion of correct
238 decisions across the population significantly decreased depending on the number of trials
239 performed during the session (i.e. as a function of the decreasing coherence in the stimulus, see
240 [Fig. 4A](#)), regardless of the motor control condition (ANCOVA, Trials: $F=199$, $p < 0.0001$;
241 Movement difficulty: $F=2.5$, $p = 0.12$; Movement difficulty x Trials: $F=0.78$, $p=0.38$, [Fig. 4C](#)). As

242 expected too, we observed that the duration of decisions (whether correct or not) increased as a
 243 function of the number of trials performed during the session (Trials: $F=32.3$, $p < 0.0001$, Fig. 4D).
 244 As mentioned above (Fig. 3, right panel), we also found a strong effect of the motor condition on
 245 the duration of the perceptual decisions, with decisions being longer when reported via movements
 246 executed toward large targets (Movement difficulty: $F=104$, $p < 0.0001$, Fig. 4D). But
 247 interestingly, we found that this effect was not dependent on the difficulty level of the perceptual
 248 decisions, even if a trend for a more pronounced impact when decisions are difficult is observed
 249 (Movement difficulty x Trials: $F=3.79$, $p = 0.052$, Fig. 4D).



250

251 **Figure 4.** A. Relationship between the number of completed trials (averaged \pm SE, shaded area, across the
 252 population) and the coherence of the decision stimulus. Coherence is defined as the ratio between the
 253 number of tokens of each color in the decision stimulus. It is expressed as the percentage of tokens of one
 254 color compared to the other. Trials are sorted chronologically and a normalization is performed by grouping
 255 them in 10 quantiles. B. Proportion of demanding movement choices as a function of decision difficulty.
 256 As in A, trials are sorted chronologically and normalized by grouping them in 10 quantiles. Because the
 257 coherence of the decision stimulus strongly co-varies with the number of completed trials, trial number is
 258 a proxy of the decision difficulty. Open circles illustrate the median values (\pm SE, gray shaded area) at the

259 population level, and light gray lines illustrate linear regressions through the data for each individual
260 subject. *C*. Median (\pm SE, colored shaded area) proportion of correct perceptual decisions across subjects,
261 as a function of decision difficulty, with trials sorted as a function of the motor condition chosen by the
262 subjects (blue: large targets/easy movement; red: small targets/difficult movement). *D*: Perceptual decision
263 durations as a function of decision difficulty, with trials sorted as a function of the motor condition chosen
264 by the subjects (blue: large targets/easy movement; red: small targets/difficult movement). Same
265 convention as in *C*.

266 DISCUSSION

267 The present study was designed to test the impact of motor demands on the accuracy and duration
268 of perceptual decisions whose difficulty was manipulated in a gradual manner, and when costly
269 movements were volitionally chosen by human subjects from one trial to the next to gain more
270 points. Our study indicates that the level of constraint associated with a movement executed to
271 express a perceptual decision strongly impacts the duration of these decisions. This influence
272 appears most important when the decisions are difficult, but it is also present for easy decisions.
273 In the following paragraphs, we discuss these results in the context of recent work on decision and
274 action interactions, and we propose an interpretation of these data in terms of behavior
275 optimization.

276 Motor constraints influence perceptual decision-making

277 Recent behavioral studies indicate that decisions and actions are closely linked, showing a high
278 level of integration during goal-directed behavior (for reviews, see [Shadmehr, 2010](#); [Gallivan et al., 2018](#);
279 [Carland et al., 2019](#); [Shadmehr et al., 2019](#); [Wispiński et al., 2020](#); [Gordon et al., 2021](#)).
280 On the one hand, the properties of movement, such as speed and duration, are influenced by
281 decision-making characteristics ([Thura et al., 2014](#); [Thura, 2020](#); [Herz et al., 2022](#), [Carsten et al.,](#)
282 [2023](#); [Saleri and Thura, 2024](#)), and the selection, preparation, and execution of movements are
283 parameterized following the same economical rules as those which govern decisional processes
284 ([Shadmehr et al., 2010](#); [Haith et al., 2012](#); [Choi et al., 2014](#); [Morel et al., 2017](#)).

285 On the other hand, numerous behavioral studies have now provided strong support for action-
286 based (or embodied) models of decision-making that hypothesize that action alternatives and their
287 associated properties, including costs, are incorporated into the choice process ([Cisek, 2007](#);
288 [Lepora and Pezzulo, 2015](#)). These behavioral studies tested the impact of motor constraints on
289 decision-making using different designs. Very often, a specific motor cost, itself manipulated in
290 different ways, is associated with each option proposed to participants during each trial, and the

291 basis for choosing varies depending on the paradigm. For example, decisions may be based
292 primarily on the motor properties of movements, with one option being costlier than the other in
293 terms of biomechanical cost or energy expenditure on each trial (Cos et al., 2011, 2014; Morel et
294 al., 2017), sometimes during ongoing actions (Michalski et al., 2020; Griebach et al., 2022;
295 Canaveral et al., 2024). In other cases, the movements performed to express a choice carry different
296 costs but the decision is primarily based on perceptual cues (Burk et al., 2014; Marcos et al., 2015;
297 Hagura et al., 2017) or rewards (Pierrieau et al., 2021; Griebach et al., 2022) associated with each
298 of the two possible options. In most of these scenarios, the manipulation of motor costs influences
299 the choice of target selected by participants before or during movement execution.

300 There is, however, evidence that questions a systematic effect of motor costs on decision making,
301 suggesting a task and/or parameter specific aspect to this phenomenon. For example, in a recent
302 study by Manzone and Welsh, the authors demonstrate that when motor costs are clearly and
303 explicitly felt by participants (which is not necessarily the case in other similar studies (Marcos et
304 al., 2015; Hagura et al., 2017)), this explicit effort has a reduced or even absent impact on
305 perceptual decision making (Manzone and Welsh, 2023). In the study of Pierrieau and colleagues,
306 the authors report that when the rewarded target carries the highest motor cost, reaching
307 movements executed within 350ms of reaction time are biased toward the other target, but this
308 effect disappears if participants takes longer to react (Pierrieau et al., 2021). Finally, when
309 comparing the effects of motor costs between a manual movement task and a walking task within
310 the same participants, Griebach and colleagues observed that the motor costs bias on perceptual
311 decisions only weakly transfer between tasks (Griebach et al., 2023). Together, these results point
312 to a contextual influence of action effort and costs on perceptual decision-making.

313 In our own recent experiments, we manipulated the motor condition in which perceptual decisions
314 were made by human or non-human subjects. Specifically, the two options offered to the
315 participants to report their choices (based on changing visual evidence) carried broadly the same
316 motor cost, but this cost varied in dedicated blocks of trials imposed on the subjects. In this case,
317 whether for human subjects or for monkeys, we observed a strong impact of the motor condition
318 on the precision and duration of the perceptual decisions taken before the arm movement was
319 executed to express these choices (Reynaud et al., 2020; Saleri Lunazzi et al., 2021; Saleri and
320 Thura, 2024).

321 Given the design-related contrasted results of the experiments mentioned above when each
322 movement option carries a specific cost, we could wonder whether in our experimental condition
323 where the two motor targets are associated with the same motor costs, the change of context,
324 notably the voluntary choice of the subjects to execute a more or less costly movement to gain
325 more or fewer points, and this possibly from one trial to another and not in blocks of several dozen
326 trials, could have consequences on the consideration of these motor costs during the perceptual
327 decision-making process. In support of action-based decision models though, we observed that not
328 only do motor costs influence decision-making when motor constraints are voluntarily chosen by
329 the subjects, often from one trial to another and not in blocks, but that this influence persists
330 whatever the difficulty of the decision, suggesting a very close and robust link between motor
331 parameters expressing a perceptual decision and the perceptual decision process.

332 [Participants seek to preserve their rate of reward](#)

333 The prospect of executing a more or less demanding movement therefore strongly and
334 systematically modulates the duration of decisions in the present experiment. But how can we
335 explain the meaning of this modulation, namely a shortening of decisions when these are expressed
336 by constrained movements? One might have expected to observe the opposite, i.e. slower and more
337 precise decisions when these choices are expressed by costly movements. Indeed, an influent
338 theory proposed that when an action is costly and requires effort, the overall motivation to behave
339 is reduced, leading to not only slower movements, but also longer reaction times (Mazzoni et al.,
340 2007; Shadmehr et al., 2019). Another interpretation of an identical result would be to consider
341 that the participants sought to optimize the efforts invested in a costly behavior. Indeed, faced with
342 a demanding movement, it is conceivable that they wanted to ensure that they made a good
343 decision by extending the duration of the deliberation, longer deliberation being usually associated
344 with better performance in stable coherence decision paradigms.

345 However, this is not what we observed. None of the 23 subjects had significantly longer decision
346 times when the movements performed to express a choice were constrained (see Fig. 3, right
347 panel). Our interpretation of the direction of this modulation is that participants sought to optimize
348 the total duration of their response, namely the duration of the decision added to that of the
349 movement. Indeed, in the experiment described in this report, the duration of each trial is entirely
350 dependent on the subject's behavior, who therefore has control over this duration and over her/his

351 speed-accuracy trade-off strategy. By choosing constrained movements to potentially gain more
352 points, participants possibly integrated that these movements requiring a higher degree of motor
353 control would be slower, in terms of duration, than less constrained movements (Fig. 2, right panel,
354 and see Fig. S1 for the analysis of movement parameters, including duration, between the two
355 motor conditions as a function of decision difficulty). Consequently, subjects possibly sought to
356 compensate for this additional time devoted to movement by shortening the duration of their
357 perceptual decisions, regardless of the difficulty of these decisions. This allows them to maximize
358 their success rate, that is, the number of successful trials, minus the effort associated with those
359 trials, divided by the time required to perform those trials. As several studies have shown, success
360 rate is a parameter that human subjects and animals seek to optimize, more than performance per
361 se, when faced with a succession of decisions and actions (Shadlen et al., 2008; Bogacz et al.,
362 2010; Balci et al., 2011; Carland et al., 2019; Shadmehr et al., 2019). Figure S2 illustrates the
363 response time (decision and movement) of the subjects as a function of the difficulty of the
364 decisions and as a function of the motor condition. Although the response time increases with the
365 increase in the difficulty of the decisions, there is no significant effect of the motor condition on
366 this overall response time. This result is consistent with a mechanism of compensation of motor
367 time costs by the duration of the decisions. Interestingly, this shortening of the decisions had no
368 impact on the precision of these decisions (Fig. 4C), which reinforces the idea that this strategy
369 was beneficial and adaptative in terms of optimizing the success rate. This observation is also
370 compatible with the idea that decisions are primarily based on information from a relatively short
371 time window (Uchida et al., 2006; Yang et al., 2008; Chittka et al., 2009). For simple color
372 discrimination, this can be as short as 30ms (Stanford et al., 2010), but even in much more difficult
373 tasks, it appears to be on the order of 100-300ms (Kiani et al., 2008; Price and Born, 2010).

374 This supposedly preponderant role of the cost of time on the behavior of the subjects does not
375 mean that effort played no role. Indeed, as mentioned above, the success rate integrates the notion
376 of effort and energy expenditure in its equation. In a recent study, we showed that just like time
377 resources, energy resources can be transferred between decision-making and motor processes, by
378 prioritizing the most critical process for the behavior in question (Leroy et al., 2023). But it also
379 appears that effort does not influence decision-making as robustly as time in an experiment
380 specifically designed to dissociate the impact of both cost types on humans decisional strategy
381 (Saleri Lunazzi et al., 2021). This is possibly because unlike time (Myerson and Green, 1995;

382 [Shadmehr et al., 2010](#)), effort, considered in its broad definition, is not always considered as a cost
383 (i.e. the effort paradox, [Inzlicht et al., 2018](#)). Even if many experiments of voluntary reaching have
384 shown that when given a choice, humans tend to prefer actions that carry the least biomechanical
385 costs over the more effortful ones ([Cos et al., 2011](#); [Marcos et al., 2015](#); [Hagura et al., 2017](#);
386 [Pierrieau et al., 2021](#); [Canaveral et al., 2024](#)), other studies have nevertheless shown that energy
387 optimization is not systematically sought by participants ([Kistemaker et al., 2010](#); [Morel et al.,](#)
388 [2017](#); [Moskowitz et al., 2023](#)). So, considering that in these particular scenarios where subjects
389 are faced with a multitude of decisions between successive (arm or eye) movements, and that the
390 time and the number of correct trials can be optimized to complete the session as quickly as
391 possible, a notion of success rate that seems to strongly influence behavior, it is time more than
392 effort that most systematically influences the strategy of the participants.

393 [Conclusions](#)

394 Taken together, the results of the present study and our past studies indicate that human subjects
395 are able to anticipate the consequence of a demanding movement to execute, when this
396 supplementary cost has been deliberately chosen on a trial-by-trial basis to potentially earn more
397 points and complete the session faster, by shortening the duration of the perceptual decisions
398 preceding the execution of the arm movements. This consideration of motor costs in decision-
399 making does not depend on the difficulty of the choices, and does not impact their precision. We
400 interpret this time compensation strategy as an adaptive way to optimize their overall rate of
401 success at the session level.

402 [METHODS](#)

403 [Participants](#)

404 Thirty-two healthy human subjects (median age \pm SD: 25.5 ± 4.2 ; 26 self-identified as females, 6
405 as males; 25 right handed) participated in this study. All subjects gave their written informed
406 consent before starting the experiment. The ethics committee of Inserm (IRB00003888,
407 IORG0003254, FWA00005831) approved the protocol on June 7th 2022. All methods were
408 performed in accordance with the relevant guidelines and regulations. Each participant was asked
409 to perform one experimental session. They received a monetary compensation (10 euros per
410 completed session) for participating in this study. All participants also performed another version
411 of the task described in the present report, on a different day, for a study designed to test the

412 hypothesis that the management of effort-related energy resources is shared between decision-
413 making and motor control (Leroy et al., 2023).

414 Experimental apparatus

415 The subjects sat in a comfortable armchair and made planar reaching movements using a handle
416 held in their dominant hand. A digitizing tablet (GTCO CalComp) continuously recorded the
417 handle horizontal and vertical positions (100 Hz with 0.013 cm accuracy). The behavioral task was
418 implemented by means of LabVIEW 2018 (National Instruments, Austin, TX). Visual stimuli and
419 handle position feedback (black cross) were projected by a DELL P2219H LCD monitor (60 Hz
420 refresh rate) onto a half-silvered mirror suspended 26 cm above and parallel to the digitizer plane,
421 creating the illusion for the participants that stimuli floated on the plane of the tablet (please see
422 Fig. 1a in Saleri Lunazzi et al., 2023).

423 Behavioral task

424 Participants performed multiple trials of a multi-step decision-making task (Fig. 1). Each trial
425 begins with a black circle (the starting circle, $\varnothing = 3\text{cm}$) displayed at the bottom of the screen. To
426 initiate a trial, the subject moves the handle in the starting circle and maintains the position for
427 300ms. A large ($\varnothing = 9\text{cm}$) circle then appears on the screen (the decision stimulus) for 300ms. It
428 contains 100 green and blue tokens. The ratio between blue and green tokens defines the coherence
429 of the decision stimulus. At this stage, the stimulus informs the subject about the difficulty of the
430 perceptual decision she/he has to make later in the trial, but the dominant color among the tokens
431 is not informative of the correct target to select at the end of the trial. The proportion of tokens of
432 the dominant color is 77% on the first trial of the session.

433 Then the decision circle disappears and two rectangles are displayed above the starting circle,
434 separated from each other by 10 cm. In each rectangle a text informs the subject about the difficulty
435 of the movement that she/he has to execute in each trial to report the perceptual decision: “1” for
436 an easy movement, executed toward a large visual target ($\varnothing = 3.75\text{cm}$, with a trial-to-trial
437 variability of 2%), or “5” for a difficult movement, executed toward a small target ($\varnothing = 1.25\text{cm}$,
438 with a trial-to-trial variability of 2%). The subject has 1s to move the handle in the chosen rectangle
439 and then must hold it for 500ms to validate this choice. She/he then returns to the starting circle
440 and maintains the position for another 500ms to continue the trial.

441 The decision circle (filled with the 100 tokens) as well as the blue and green movement targets
442 then appear. The movement targets are visual circles displayed 180° apart of the starting circle.
443 Their size depends on the choice of the subject, either large ($\emptyset = 3.75\text{cm}$) or small ($\emptyset = 1.25\text{cm}$).
444 The distance between the starting circle center and each movement target center was 10cm, with
445 a trial-to-trial variability of 1.9cm. The dominant color among the tokens (with the same proportion
446 as at the beginning of the trial) now determines the correct target to select.

447 The subject task is to determine the dominant color in the decision circle, either blue or green. To
448 express this perceptual decision, the participant moves the handle in the lateral target whose color
449 corresponds to her/his choice and maintains this position for 500ms. The dominant color (blue or
450 green) as well as the position of the green and blue movement targets relative to the starting circle
451 are randomized from trial to trial. The maximum decision duration allowed (the time between the
452 decision circle onset and movement onset) is 1s. The maximum movement duration allowed (the
453 time between movement onset and offset) is 750ms.

454 At the end of the trial, a visual cue informs the subject about the outcome of the trial. The chosen
455 target was surrounded by a green circle if she/he accurately reaches the correct target, and by a red
456 one if she/he accurately reaches the wrong target. The subject earns the number of points
457 corresponding to the chosen difficulty of the movement to execute if the correct target was
458 accurately reached. The goal of the subject is to earn a total of 200 points. If the subject fails to
459 reach or stop in the chosen target (inaccurate movement, whether it is the correct target or not),
460 the number of points chosen at the beginning of the trial is subtracted. Regardless of the movement
461 constraint level chosen by the subject, if she/he selects the wrong target (decision error) with an
462 accurate movement, points are not deducted. To move on to the next trial, the subject moves the
463 handle back in the starting circle and maintains the position for 500ms.

464 In this experiment, the number of points accumulated by the subject determines the coherence of
465 the decision stimulus. The coherence of the decision stimulus is initially set to 77% at the
466 beginning of the session and it linearly decreases with the accumulation of points, reaching 51%
467 at 200 points. As a consequence, the difficulty of decision progressively increases as the subject
468 gets close to 200 points. We expected to observe with this design a mixture of choices of the
469 difficulty of the movements to be performed to express the perceptual decisions, regardless of the

470 coherence of the decision stimulus, with a bias for the most difficult movements chosen more
471 frequently at the beginning of the session (when perceptual decisions are easier) than at the end.

472 [Instructions provided to the subjects](#)

473 To familiarize each participant with the task and with the manipulation of the handle on the tablet,
474 a training phase was proposed prior to the experimental phase per se. During this training phase,
475 subjects performed about 20 training trials where they could choose the difficulty of the movement
476 to make (easy or difficult) and report moderately difficult (63% coherence) perceptual decisions
477 by executing reaching movements to those targets. The training phase was prolonged if subjects
478 required so. During the experimentation phase, each subject was instructed to perform the task
479 described above and they were informed that they needed to earn a total of 200 points to complete
480 the session. Importantly, the 32 subjects who performed the task were not told about the decreasing
481 coherence of the decision stimulus indexed to the accumulation of points. They were also not told
482 about their number of points accumulated after each trial. We informed the subjects that there
483 would be no scheduled breaks during the session, except in case of discomfort or real fatigue. No
484 subject requested a break during their session.

485 [Data analysis and statistics](#)

486 Data were collected by means of LabVIEW 2018 (National Instruments, Austin, TX), stored in a
487 database (Microsoft SQL Server 2005, Redmond, WA), and analyzed off-line with custom-written
488 MATLAB scripts (MathWorks, Natick, MA).

489 Arm movement characteristics were assessed using the subjects' movement kinematics.
490 Horizontal and vertical arm position data (collected from the handle on the digitizing tablet) were
491 first filtered using a tenth-degree polynomial filter and then differentiated to obtain a velocity
492 profile. Onset and offset of movements were determined using a 3.75 cm/s velocity threshold. Peak
493 velocity and amplitude was determined as the maximum value and the Euclidian distance between
494 movement onset and offset, respectively.

495 An accurate movement is defined as a movement that reached a target (whether it is the correct
496 target or not) and stayed in it for 500ms. In this report we only refer to movements executed to
497 report the perceptual decisions (not those executed to select the difficulty of the movement to
498 perform to report the perceptual decisions). Decision duration is defined as the time between the
499 onset of the stimulus providing the visual evidence to the subject (the decision circle containing

500 the 100 tokens) to the onset of the movement executed to report the decision. A decision is defined
501 as correct if the correct target is chosen, regardless of the accuracy of the movement.

502 Chi-squared tests for independence were used to assess the effect of movement difficulty
503 (constrained or less constrained) on individual subjects' movement and decision accuracy.
504 Wilcoxon rank sum tests were used to assess the effect of movement constraint level on individual
505 subjects' decision and movement duration. Chi-squared tests for independence were used to test
506 the effect of decision difficulty, evaluated by chronologically grouping trials in 10 quantiles, on
507 individual subjects' proportion of constrained movement choices. At the population level, Kruskal-
508 Wallis tests were used to test the effect of decision difficulty on the proportion of constrained
509 movement choices. Analyses of covariance (ANCOVAs) were used to assess the effect of decision
510 difficulty, motor constraint level and their interaction on decision accuracy and duration. The
511 significance level of all statistical tests was set at 0.05, and highest levels of significance are
512 reported when appropriate.

513 AUTHORS' CONTRIBUTION

514 EL, EK and DT designed the experiment

515 EK coded the task

516 EL collected the data

517 EL and DT conducted the analyses and prepared the figures

518 DT wrote the draft of the manuscript

519 EL, EK and DT revised the draft and approved the final version of the manuscript

520 CONFLICT OF INTEREST STATEMENT

521 The authors declare no competing financial interests.

522 DATA AVAILABILITY STATEMENT

523 The datasets used and/or analyzed during the current study are available from the corresponding
524 author on reasonable request.

525 REFERENCES

- 526 Balci F, Simen P, Niyogi R, Saxe A, Hughes JA, Holmes P, Cohen JD (2011) Acquisition of
527 decision making criteria: reward rate ultimately beats accuracy. *Atten Percept Psychophys*
528 73:640–657.
- 529 Bogacz R, Hu PT, Holmes PJ, Cohen JD (2010) Do humans produce the speed–accuracy trade-off
530 that maximizes reward rate? *Quarterly Journal of Experimental Psychology* 63:863–891.
- 531 Burk D, Ingram JN, Franklin DW, Shadlen MN, Wolpert DM (2014) Motor Effort Alters Changes
532 of Mind in Sensorimotor Decision Making Kiebel S, ed. *PLoS ONE* 9:e92681.
- 533 Canaveral CA, Lata W, Green AM, Cisek P (2024) Biomechanical costs influence decisions made
534 during ongoing actions. *Journal of Neurophysiology* 132:461–469.
- 535 Carland MA, Thura D, Cisek P (2019) The Urge to Decide and Act: Implications for Brain
536 Function and Dysfunction. *Neuroscientist*:107385841984155.
- 537 Carsten T, Fievez F, Duque J (2023) Movement characteristics impact decision-making and vice
538 versa. *Sci Rep* 13:3281.
- 539 Chittka L, Skorupski P, Raine NE (2009) Speed–accuracy tradeoffs in animal decision making.
540 *Trends in Ecology & Evolution* 24:400–407.
- 541 Choi JES, Vaswani PA, Shadmehr R (2014) Vigor of Movements and the Cost of Time in Decision
542 Making. *Journal of Neuroscience* 34:1212–1223.
- 543 Cisek P (2007) Cortical mechanisms of action selection: the affordance competition hypothesis.
544 *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:1585–1599.
- 545 Cos I, Bélanger N, Cisek P (2011) The influence of predicted arm biomechanics on decision
546 making. *Journal of Neurophysiology* 105:3022–3033.
- 547 Cos I, Duque J, Cisek P (2014) Rapid prediction of biomechanical costs during action decisions.
548 *Journal of Neurophysiology* 112:1256–1266.
- 549 Franklin DW, Wolpert DM (2011) Computational mechanisms of sensorimotor control. *Neuron*
550 72:425–442.
- 551 Gallivan JP, Chapman CS, Wolpert DM, Flanagan JR (2018) Decision-making in sensorimotor
552 control. *Nat Rev Neurosci* 19:519–534.
- 553 Gold JJ, Shadlen MN (2007) The Neural Basis of Decision Making. *Annu Rev Neurosci* 30:535–
554 574.
- 555 Gordon J, Maselli A, Lancia GL, Thiery T, Cisek P, Pezzulo G (2021) The road towards
556 understanding embodied decisions. *Neuroscience & Biobehavioral Reviews* 131:722–736.
- 557 Griebbach E, Raßbach P, Herbort O, Cañal-Bruland R (2022) Embodied decisions during walking.
558 *J Neurophysiol* 128:1207–1223.
- 559 Griebbach E, Raßbach P, Herbort O, Cañal-Bruland R (2023) Embodied decision biases:
560 individually stable across different tasks? *Exp Brain Res* 241:1053–1064.
- 561 Hagura N, Haggard P, Diedrichsen J (2017) Perceptual decisions are biased by the cost to act.
562 *eLife* 6:e18422.
- 563 Haith AM, Reppert TR, Shadmehr R (2012) Evidence for Hyperbolic Temporal Discounting of
564 Reward in Control of Movements. *Journal of Neuroscience* 32:11727–11736.

565 Herz DM, Bange M, Gonzalez-Escamilla G, Auer M, Ashkan K, Fischer P, Tan H, Bogacz R,
566 Muthuraman M, Groppa S, Brown P (2022) Dynamic control of decision and movement
567 speed in the human basal ganglia. *Nat Commun* 13:7530.

568 Inzlicht M, Shenhav A, Olivola CY (2018) The Effort Paradox: Effort Is Both Costly and Valued.
569 *Trends in Cognitive Sciences* 22:337–349.

570 Kiani R, Hanks TD, Shadlen MN (2008) Bounded Integration in Parietal Cortex Underlies
571 Decisions Even When Viewing Duration Is Dictated by the Environment. *J Neurosci*
572 28:3017–3029.

573 Kistemaker DA, Wong JD, Gribble PL (2010) The central nervous system does not minimize
574 energy cost in arm movements. *J Neurophysiol* 104:2985–2994.

575 Lee D, Seo H, Jung MW (2012) Neural Basis of Reinforcement Learning and Decision Making.
576 *Annu Rev Neurosci* 35:287–308.

577 Lepora NF, Pezzulo G (2015) Embodied Choice: How Action Influences Perceptual Decision
578 Making Daunizeau J, ed. *PLoS Comput Biol* 11:e1004110.

579 Leroy É, Koun É, Thura D (2023) Integrated control of non-motor and motor efforts during
580 perceptual decision-making and action execution: a pilot study. *Sci Rep* 13:9354.

581 Manzone JX, Welsh TN (2023) Explicit effort may not influence perceptuomotor decision-
582 making. *Exp Brain Res* 241:2715–2733.

583 Marcos E, Cos I, Girard B, Verschure PFMJ (2015) Motor Cost Influences Perceptual Decisions
584 Gribble PL, ed. *PLoS ONE* 10:e0144841.

585 Mazzoni P, Hristova A, Krakauer JW (2007) Why Don't We Move Faster? Parkinson's Disease,
586 Movement Vigor, and Implicit Motivation. *Journal of Neuroscience* 27:7105–7116.

587 Michalski J, Green AM, Cisek P (2020) Reaching decisions during ongoing movements. *Journal*
588 *of Neurophysiology* 123:1090–1102.

589 Morel P, Ulbrich P, Gail A (2017) What makes a reach movement effortful? Physical effort
590 discounting supports common minimization principles in decision making and motor control
591 Rushworth M, ed. *PLoS Biol* 15:e2001323.

592 Moskowitz JB, Berger SA, Fooker J, Castelhana MS, Gallivan JP, Flanagan JR (2023) The
593 influence of movement-related costs when searching to act and acting to search. *Journal of*
594 *Neurophysiology* 129:115–130.

595 Myerson J, Green L (1995) Discounting of delayed rewards: Models of individual choice. *J Exp*
596 *Anal Behav* 64:263–276.

597 Pierrieau E, Lepage J-F, Bernier P-M (2021) Action Costs Rapidly and Automatically Interfere
598 with Reward-Based Decision-Making in a Reaching Task. *eNeuro* 8:ENEURO.0247-
599 21.2021.

600 Price NSC, Born RT (2010) Timescales of sensory- and decision-related activity in the middle
601 temporal and medial superior temporal areas. *J Neurosci* 30:14036–14045.

602 Reynaud AJ, Saleri Lunazzi C, Thura D (2020) Humans sacrifice decision-making for action
603 execution when a demanding control of movement is required. *Journal of Neurophysiology*
604 124:497–509.

605 Saleri C, Thura D (2024) Evidence for interacting but decoupled controls of decisions and
606 movements in non-human primates. *J Neurophysiol*.

607 Saleri Lunazzi C, Reynaud AJ, Thura D (2021) Dissociating the Impact of Movement Time and
608 Energy Costs on Decision-Making and Action Initiation in Humans. *Front Hum Neurosci*
609 15:715212.

610 Saleri Lunazzi C, Thura D, Reynaud AJ (2023) Impact of decision and action outcomes on
611 subsequent decision and action behaviours in humans. *European Journal of Neuroscience*
612 57:1098–1113.

613 Shadlen MN, Kiani R, Hanks TD, Churchland AK (2008) Neurobiology of decision making: An
614 intentional framework. In: *Better than conscious? Decision making, the human mind, and*
615 *implications for institutions*, pp 71–101 Strüngmann Forum reports. Cambridge, MA, US:
616 MIT Press.

617 Shadmehr R (2010) Control of movements and temporal discounting of reward. *Current Opinion*
618 *in Neurobiology* 20:726–730.

619 Shadmehr R, Krakauer JW (2008) A computational neuroanatomy for motor control. *Exp Brain*
620 *Res* 185:359–381.

621 Shadmehr R, Orban de Xivry JJ, Xu-Wilson M, Shih T-Y (2010) Temporal Discounting of Reward
622 and the Cost of Time in Motor Control. *Journal of Neuroscience* 30:10507–10516.

623 Shadmehr R, Reppert TR, Summerside EM, Yoon T, Ahmed AA (2019) Movement Vigor as a
624 Reflection of Subjective Economic Utility. *Trends in Neurosciences* 42:323–336.

625 Stanford TR, Shankar S, Massoglia DP, Costello MG, Salinas E (2010) Perceptual decision
626 making in less than 30 milliseconds. *Nature Neuroscience* 13:379–385.

627 Thura D (2020) Decision urgency invigorates movement in humans. *Behavioural Brain Research*
628 382:112477.

629 Thura D, Cos I, Trung J, Cisek P (2014) Context-dependent urgency influences speed-accuracy
630 trade-offs in decision-making and movement execution. *J Neurosci* 34:16442–16454.

631 Uchida N, Kepecs A, Mainen ZF (2006) Seeing at a glance, smelling in a whiff: rapid forms of
632 perceptual decision making. *Nat Rev Neurosci* 7:485–491.

633 Wispinski NJ, Gallivan JP, Chapman CS (2020) Models, movements, and minds: bridging the gap
634 between decision making and action. *Ann NY Acad Sci* 1464:30–51.

635 Yang Y, DeWeese MR, Otazu GH, Zador AM (2008) Millisecond-scale differences in neural
636 activity in auditory cortex can drive decisions. *Nat Neurosci* 11:1262–1263.