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Action costs rapidly and automatically interfere with reward-based decision-making in a reaching task

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1 **Title: Action costs rapidly and automatically interfere with reward-based decision-making**
2 **in a reaching task**

3 *Abbreviated title:* Influence of action costs on reward-based choices

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21 **ABSTRACT**

22 It is widely assumed that we select actions we value the most. While the influence of rewards
23 on decision-making has been extensively studied, evidence regarding the influence of motor
24 costs is scarce. Specifically, how and when motor costs are integrated in the decision process
25 is unclear. Twenty-two right-handed human participants performed a reward-based target
26 selection task by reaching with their right arm toward one of two visual targets. Targets were
27 positioned in different directions according to biomechanical preference, such that one target
28 was systematically associated with a lower motor cost than the other. Only one of the two targets
29 was rewarded, either in a congruent or incongruent manner with respect to the associated motor
30 cost. A timed-response paradigm was used to manipulate participants' reaction times (RT).
31 Results showed that when the rewarded target carried the highest motor cost, movements
32 produced at short RT (<350ms) were deviated toward the other (i.e., non-rewarded, low-cost)
33 target. In this context participants needed an additional 150ms delay to reach the same
34 percentage of rewarded trials as when the low-cost target was rewarded. Crucially, motor costs
35 affected the total earnings of participants. These results demonstrate a robust interference of
36 motor costs in a simple reward-based decision-making task. They point to the rapid and
37 automatic integration of motor costs at an early stage of processing, potentially through the
38 direct modulation of competing action representations in parieto-frontal regions. The
39 progressive overcoming of this bias with increasing RT is likely achieved through top-down
40 signaling pertaining to expected rewards.

41

42 SIGNIFICANCE STATEMENT

43 Rapid evaluation of expected action costs for action selection possesses an adaptive value in
44 ecological settings. The present work shows that these motor costs quickly and automatically
45 bias decisions supposedly based on reward information, leading to lesser earnings when
46 rewards and motor costs are incongruent. This bias is progressively overcome with increasing
47 reaction times, consistent with the perspective of a hierarchical influence of different decisional
48 variables on action representations based on their level of abstraction. Overall, these findings
49 highlight the need to consider motor costs when using dynamic motor tasks for studying
50 decision-making, especially under temporal pressure.

51

52 INTRODUCTION

53 Should I run after the bus or wait for the next one? Should I grasp the pen on my right
54 side or the one on my left? Motor decisions shape our daily life, allowing us to interact with
55 our environment by selecting the actions we ultimately make (Cisek & Kalaska, 2010). Action
56 selection is determined by optimization rules (Todorov & Jordan, 2002; Scott et al, 2012) in
57 order to maximize a reward rate which defines the action value (Rangel & Hare, 2010; Carland
58 et al, 2019). Hence action selection is often studied in paradigms manipulating action values,
59 also called value-based decision making. Value-based decision making has mostly been
60 investigated by varying the type, size and probability of reward as well as the influence of time
61 (Padoa-Schioppa & Assad, 2006; Klein-Flugge et al, 2012; Kable & Glimcher, 2007).
62 Intriguingly, the involvement of the expected motor costs associated with each possibility of
63 action, another fundamental parameter of the reward rate (Rangel & Hare, 2010; Carland et al,
64 2019), has been less studied and remains poorly understood, both at the behavioral (Morel et
65 al, 2017) and neuronal levels (Walton & Bouret, 2018).

66 Understanding the integration of motor costs in the action selection process represents an
67 important stake for the development of an ecological model of decision-making. Indeed,
68 considering motor costs quickly and reliably is crucial when one has to flee from a predator or
69 when hunting a prey. Inspired by these accounts, it has been suggested that sensorimotor
70 representations of action possibilities, called affordances (Gibson, 1966), might be encoded and
71 compete for action selection in parieto-frontal regions (Cisek, 2012; Gallivan et al, 2015;
72 Pezzulo & Cisek, 2016). An intriguing possibility is that motor costs quickly modulate the early
73 formation of action representations and/or the competition process taking place in parieto-
74 frontal regions, and thus automatically bias action selection, even when it is supposed to rely
75 on abstract or cognitive rules. This possibility is supported by recent behavioral studies

76 demonstrating that motor costs strongly influence target selection in motor choices (Cos et al,
77 2011, Shadmehr et al, 2016; Gallivan et al, 2018) even when adding temporal pressure (Cos et
78 al, 2014), and can also significantly bias perceptual-based judgements (Marcos et al, 2015;
79 Hagura et al, 2017). Yet, these preceding studies have revealed a significant influence of motor
80 costs only in uncertain perceptual decision-making contexts, that is when the information
81 provided by visual stimuli is blurred and the perceptual decision harder. In these contexts, motor
82 costs might have influenced decisions because of the lack of clear perceptual evidence favoring
83 one of the options dictated by the abstract rule, thus making the less effortful option the most
84 valued.

85 Hence, these evidence do not permit to disentangle if motor costs involve an automatic
86 bias even when the decision is based on a clear and explicit abstract rule. To test that we
87 developed a simple reward-based decision-making paradigm where the perceptual evidence
88 remained the same across conditions and constant during trials. Critically, motor costs were
89 manipulated by varying target positions in the workspace to influence the biomechanical
90 complexity of the required reaching movement, and thus the amount of effort needed. We
91 hypothesized that if motor costs automatically bias decisions, then there should be a significant
92 influence of target position on choices even though the level of perceptual evidence remains
93 constant. We further assumed that this bias would be most apparent at short response latencies.
94 In order to ensure a sufficient number of trials with short reaction times and to better identify
95 the latency at which motor costs might bias behavior, we used a timed-response task (Ghez et
96 al, 1997; Cos et al, 2014; Haith et al, 2016). Results revealed that motor costs had a significant
97 influence on participants' behavior by impacting movement kinematics and target choices, and
98 thus modulating the amount of rewards ultimately gained.

99 MATERIALS AND METHODS

100 **Participants**

101 Twenty-two university students (10 females, 24 ± 4 (mean \pm SD) years old) participated
102 in this study. All participants had normal or corrected-to-normal vision. All were right-handed
103 based on self-report and were free of any known neurological or psychiatric condition. A \$30
104 CAD compensation was given to participants (\$15 per one-hour session) and they could earn
105 up to an additional \$20 CAD, depending on their performance. In all cases, participants finished
106 the experiment with a net monetary gain averaging $\$44.5 \pm 1.8$. Participants gave their informed
107 written consent, and all procedures were approved by the University of Sherbrooke institutional
108 review board and ethics committee. The experiment conformed to the standards set by the 1964
109 Declaration of Helsinki.

110 **Experimental task**

111 *Set-up.* The experimental setup consisted of a table supporting a 20-inch computer
112 monitor that projected visual stimuli onto a mirror positioned horizontally in front of the
113 participants. The monitor (Dell P1130 20-inch monitor; resolution: 1024×768 ; refresh rate:
114 150 Hz) was mounted face down 29 cm above the mirror and the mirror was positioned 29 cm
115 above the table surface. A two-joint manipulandum composed of two lightweight metal rods
116 with two potentiometers located at the manipulandum's hinges permitted to record participants
117 movements with an acquisition frequency of 100 Hz. Participants were asked to grasp a short
118 handle located at the mobile end of the manipulandum, which position in the workspace was
119 visible for the participants via a cursor projected on the monitor. Consequently, although
120 participants could not see their right hand, they had constant visual feedback of the position of
121 their hand, in a manner similar to a computer mouse. This set-up allowed participants to see the

122 visual stimuli in the same plane as their hand and has already been used in published studies
123 (Hamel et al, 2017; Hamel-Thibault et al, 2018; Savoie et al, 2019).

124 *Overview.* Participants were seated in front of this set-up. They were asked to reach
125 toward visual targets (diameter: 3 cm) with their right hand. Their starting position was
126 controlled by resting their chin on a small support and keeping their right elbow in contact with
127 the surface of the table. They were also told to minimize postural changes during the
128 experiment. To initiate a trial, participants had to place the cursor (white circle, diameter: 0.6
129 cm), and thus their hand, on a starting point located at the center of the screen (gray circle,
130 diameter: 0.6 cm). Most of the trials (720/1200) were two-target trials (2T) that consisted of
131 two targets located 90° apart on the screen, and the rest of the trials (480/1200) were one-target
132 trials (1T) in which only one target was displayed. The difference between the two conditions
133 is that in 2T participants had to choose which target they wanted to reach. There were four
134 possible target locations: 60°, 150°, 240° and 330°. All targets were at the same distance from
135 the starting point (10 cm). In 2T, targets could appear upward (CONF1), leftward (CONF2),
136 downward (CONF3) or rightward (CONF4) from the starting point. Each of these
137 configurations contained one target located in a direction biomechanically easier to reach than
138 the other (see below). The order of presentation of the trials was varied pseudo-randomly by
139 ensuring that the same condition was not presented twice consecutively and that a 2T trial
140 following a 1T trial did not consist of a configuration that included the same target as the one
141 displayed in the 1T trial, in order to prevent repetitiveness of choices. Because the deliberation
142 time was constrained (see below), the use of different configurations of targets provided
143 stochasticity and prevented the stereotypical preplanning of any given movement. Six blocks
144 of 200 test trials were used for each participant. The experiment was divided into 2 one-hour
145 sessions (3 blocks per session) separated by 24 hours. During the first session, participants had
146 to perform at least two blocks of 20 familiarization trials before beginning the experimental

147 blocks. If they succeeded at correctly hitting targets in 15 out of 20 trials in the second block,
148 they were allowed to move on with the first block of test trials, otherwise they had to perform
149 another familiarization block of 20 trials.

150 *Trial timeline.* We used a timed-response task (Ghez et al, 1997; Cos et al, 2014; Haith
151 et al, 2016) to control participants' reach reaction times. During each trial, participants heard a
152 sequence of four rhythmic auditory tones separated by 500 ms intervals (Figure 1A). The first
153 tone was triggered after holding the cursor on the starting point for 350 ms. Targets were
154 projected 100 ms to 400 ms before the fourth tone, according to a uniform distribution (60 trials
155 per condition ranging from 100 ms to 400 ms with a 5 ms increment). Participants were told to
156 initiate their movement as synchronously as possible with the fourth tone. Visual feedback was
157 presented at movement end and remained for 1 s. In correct trials, the feedback indicated the
158 number of points won (between 0 and 1 depending on MT when a green target was correctly
159 reached or 0 when it was a cyan target, see below for further details). Trials in which participants
160 initiated their movement more than 150 ms before or after the fourth tone were aborted and an
161 error message was presented, informing them that they had lost 1 point because they were too
162 fast or too slow. The diameter of the targets was relatively large (3 cm) in order to minimize a
163 potential precision bias which could interfere with the influence of biomechanical costs on
164 decisions (Cos et al, 2012). Accordingly, there was no penalty for missed-target trials, an error
165 message simply indicated that the participant had won no point because the target was missed.
166 Once the movement ended, participants had to bring the cursor back to the starting point to
167 initiate the next trial.

168 *Manipulation of rewards and costs.* Each reaching movement has a biomechanical cost
169 that depended on the direction of the movement in regard to the ellipse of mobility of the right
170 arm in our task. Indeed, previous studies showed that targets located on the major axis of the
171 ellipse of mobility (60° and 240°) are chosen more often than targets located on the minor axis

172 (150° and 330°), because their associated reaching movement carries a lower biomechanical
173 cost (Cos et al, 2011; Shadmehr et al, 2016; Michalski et al, 2020; Figure 1B). Importantly, in
174 each 2T configuration one target was located on the major axis of the ellipse of mobility of the
175 participant's arm and thus associated with a low biomechanical cost (LC), whereas the other
176 was located on the minor axis and considered as a high-cost target (HC). Hence, there was a
177 difference of motor costs between the two action possibilities. Participants were not told that
178 some targets were more costly to reach than others. Targets could appear green or cyan, with
179 an equal level of luminance. Participants were told that green targets were rewarded (1 point)
180 whereas cyan targets were not, and that the cumulated points would be converted into net
181 earnings at the end of the experiment (42 points = \$1 CAD). Additionally, to incentivize speed,
182 the magnitude of reward on a trial gradually decreased as a function of movement time; if the
183 movement time was above 250 ms, the reward was decreased by 0.2 points per additional 100
184 ms. Thus, in 2T condition, the manipulation of reward and motor cost could be congruent
185 (CONG) when the LC target was green (rewarded) and the HC target was cyan (non-rewarded),
186 or on the contrary it could be incongruent (INCONG) when the HC target was green and the
187 LC target was cyan. There also was a control condition (CTRL) in which both targets were the
188 same color, so that the participants' decision should be based exclusively on the difference in
189 motor costs between targets (Figure 1C).

190

191 **[Insert Figure 1]**

192

193 **Data analysis**

194 Visual stimuli were presented using Psychtoolbox on Matlab (Mathworks). Hand
195 position was estimated in real time with the coordinates of the two potentiometers in the

196 workspace. Movement onset was defined as the first time point when the coordinates of the
197 hand were outside the starting point. Movement end was defined as the first time point when
198 the coordinates of the hand were recorded inside of one of the presented targets with a velocity
199 below 1 pixel/s. Trials where movement velocity fell below 1 pixel/s outside of the presented
200 targets were considered as missed-target trials. Reaction times (RT) were calculated as the
201 latency between target appearance and movement onset. Movement times (MT) were calculated
202 as the latency between movement onset and movement end. In 2T trials, the target where the
203 movement ended was considered as the final choice of participants. Importantly, because of the
204 possibility of rapid influence of motor costs on choices (Cos et al, 2014) and changes-of-mind
205 during movement (Resulaj et al, 2009), we investigated the initial choice of participants. The
206 initial choice was determined according to which quadrant the hand was located 100 ms after
207 movement onset. Missed-target trials where the hand position at movement end was less than
208 1 cm around the edges of one of the targets (less than 4 cm from the target center) were kept
209 for further analysis. Indeed, because there was a consequent proportion of missed-target trials
210 (~9%) due to the high time pressure, and because we were mainly interested in target choices
211 and not in movement accuracy, we considered that movements ending less than 1 cm around a
212 target indicated that this target was chosen by the participant. Participants had to initiate their
213 movements in a time window of 300 ms centered on the go cue (fourth tone) or else the trial
214 was aborted and they lost 1 point (see above). Hence, these error trials were also excluded from
215 the analysis. 2T trials for which the trajectory angle 100 ms after movement onset was outside
216 of the quadrants containing the targets ($\pm 45^\circ$ from the target) were excluded from analysis
217 (0.3% of 2T trials) to ensure that the observed action was not the result of a default or pre-
218 planned response. 1T trials for which the trajectory angle 100 ms after movement onset was
219 more than 90° from the target were excluded (0.2% of 1T trials). The difference in accuracy
220 criterion between 1T and 2T trials was chosen in order to make both conditions comparable.

221 Indeed, we reasoned that to control whether a rapid bias toward the low-cost direction was the
222 result of a pre-planned movement or a deviated trajectory to reach the high-cost target, we
223 should keep IT trials in which the trajectory would have been deviated in these directions.

224 **Experimental design and statistical analysis**

225 All analyses were conducted on the 22 participants that took part in the experiment. In
226 order to take into account interindividual variability in behavior, we used general linear mixed
227 models (GLMM) instead of ANOVA for within-subjects comparisons. Indeed, GLMM allow
228 to analyze data with different numbers of observations per subject and condition by assigning
229 participants as a random factor in the model, making it a robust approach for the analysis of
230 biological data (Harrison et al, 2018). For each analysis we ran several models including the
231 different combinations of fixed and random factors and interactions between them. We then
232 selected the model with the lowest Akaike Information Criterion (AIC). AIC is a statistic that
233 quantifies the loss of information resulting from modeling the real process underlying the data
234 by taking into account concurrently the bias and the variance of the model (Symonds &
235 Moussali, 2010). Importantly, all GLMM that we used included Subject (22 levels: one for each
236 participant) as a random variable. We used paired t-tests or Wilcoxon tests if the data were not
237 normally distributed ($p < 0.05$ Shapiro-Wilk test) for pairwise comparisons. A Bonferroni
238 correction of p-values was applied when conducting multiple pairwise comparisons. For each
239 statistical test conducted, Cohen's d was reported to indicate effect size (Lakens, 2013).
240 Statistical analyses were computed using Jamovi v.1.2.27 (the jamovi project (2019). *Jamovi*.
241 [Computer software]. Retrieved from <https://www.jamovi.org>), a software that implements R
242 statistical language (R Core Team (2018). R: A language and environment for statistical
243 computing. [Computer software]. Retrieved from <https://www.cran.r-project.org/>).

244 RESULTS

245 We first sought to verify whether motor costs had a significant influence on participants'
246 movements and choices when targets were equally valued. To do so, we isolated both 1T and
247 2T trials in the CTRL condition. Targets in positions 1 and 3 were located on the major axis of
248 the ellipse of mobility and thus associated with a low biomechanical cost (LC), whereas targets
249 in positions 2 and 4 were on the minor axis and considered as high-cost targets (HC) (see
250 Material and method, Figure 1B). Targets were rewarded or not depending on their color (cyan:
251 no reward, green: reward). GLMM that included Position (4 levels: POS1, POS2, POS3 and
252 POS4) and Color (2 levels: Cyan or Green) were conducted on MT in 1T trials. The selected
253 GLMM ($MT \sim 1 + \text{Position} + \text{Color} + \text{Position}:\text{Color} + (1 + \text{Position} | \text{Sujet})$, $AIC = -36593.1$,
254 $BIC = -36373.8$, marginal $R^2 = 0.23$, conditional $R^2 = 0.53$) showed a significant effect of the
255 position of the target on MT ($F(3,21) = 128.0$, $p < 10^{-5}$), but neither an effect of color
256 ($F(1,9847.7) = 0.03$, $p = 0.858$) nor an interaction between them ($F(3,9847.9) = 0.8$, $p = 0.519$).
257 Post-hoc analyses showed that MT in 1T trials were significantly lower for movements directed
258 to target position 1 compared to targets located in position 2 ($t(21) = -15.4$, $p < 10^{-5}$, Cohen's d
259 $= -3.3$) and position 4 ($t(21) = -14.3$, $p < 10^{-5}$, Cohen's $d = -3.1$). Similarly, movements directed
260 to target position 3 were significantly faster than those directed to targets in position 2 ($t(21) =$
261 -16.2 , $p < 10^{-5}$, Cohen's $d = -3.5$) and position 4 ($t(21) = -12.8$, $p < 10^{-5}$, Cohen's $d = -2.7$), thus
262 globally showing that MT was reduced when reaching to LC as compared to HC targets (Figure
263 2A).

264 In 2T trials, the potential decisional bias incurred by motor costs was assessed using
265 one-sample Wilcoxon-ranked tests on the average proportion of LC target choices across
266 participants in the CTRL condition for each configuration of targets. Precisely, the statistical
267 test aimed to determine if the proportion of LC target choices was significantly different from
268 50%. Results showed that participants' choices were significantly biased toward the LC targets,

269 regardless of the configuration (CONF1: $W(21) = 253$, $p < 10^{-5}$, Cohen's $d = 2.3$; CONF2:
270 $W(21) = 243$, $p = 10^{-4}$, Cohen's $d = 1.7$; CONF3: $W(21) = 238$, $p = 10^{-4}$, Cohen's $d = 1.2$;
271 CONF4: $W(21) = 253$, $p < 10^{-5}$, Cohen's $d = 2.0$; Figure 2B). Note that participants tended to
272 choose more often the LC target in 2T rewarded trials compared to non-rewarded trials ($t(21)$
273 $= 3.3$, $p = 0.003$, Cohen's $d = 0.7$) but the mean difference between choices was low (3.8%)
274 and was not sufficient to significantly impact the average MT between rewarded and non-
275 rewarded trials ($t(21) = 0.4$, $p = 0.672$). Furthermore, a control analysis conducted only on non-
276 rewarded CTRL trials also showed a significant preference for LC targets (CONF1: $W(21) =$
277 238 , $p = 10^{-4}$, Cohen's $d = 1.3$; CONF2: $W(21) = 249$, $p = 10^{-4}$, Cohen's $d = 1.9$; CONF3: $W(21)$
278 $= 247$, $p = 10^{-4}$, Cohen's $d = 1.7$; CONF4: $W(21) = 249$, $p = 10^{-4}$, Cohen's $d = 1.9$). These first
279 results confirm that participants' movements and choices were significantly influenced by the
280 differential motor costs associated with each target in our task, which replicates previous
281 findings using similar tasks (Cos et al, 2011, 2014; Shadmehr et al, 2016).

282

283

[Insert Figure 2]

284

285 The next step of the analyses consisted in testing the influence of motor costs on reward-
286 based decisions. Specifically, we aimed to compare the accuracy of the decisions in CONG and
287 INCONG conditions. We analyzed initial choices by calculating the trajectory angle 100 ms
288 after movement onset and comparing it with the actual angle of the rewarded target in each
289 condition (Figure 3A). The success rate was defined as the proportion of trials oriented toward
290 the quadrant of the rewarded target 100 ms after movement onset. Consequently, trials with
291 movements initiated (100 ms after movement onset) in the quadrant of the rewarded target were
292 considered as correct and trials with movements initiated in the quadrant of the non-rewarded
293 target were considered as incorrect. Globally, participants were less accurate in INCONG than

294 in CONG trials, their success rates being lower in the former condition ($W(21) = 253$, $p = 10^{-4}$,
295 Cohen's $d = 1.1$; Figure 3B). In order to probe the magnitude of this difference for the different
296 deliberation periods, we then computed the success rates of participants according to their RT.
297 As expected, the success rates increased with the length of RT, but this rise appeared slower in
298 the INCONG condition than in the CONG condition (Figure 3C). Because we used the hand
299 trajectory to define choices, we controlled for any default bias that could be due to the position
300 of the target by adding 1T trials to the model. More specifically, we used rewarded 1T trials,
301 split according to their motor cost (R-HC and R-LC). Thus, the only difference between
302 INCONG and R-HC trials was the presence of the non-rewarded LC target in the INCONG
303 condition (in the same way the presence of the non-rewarded HC target in the CONG condition
304 when comparing CONG and R-LC trials). The analysis demonstrated that success rates were
305 significantly modulated both by conditions and RT (Figure 3C). We used a GLMM with
306 Condition (4 levels: CONG, INCONG, R-LC and R-HC) and RT (13 levels: 20-ms bins ranging
307 from 200 to 460 ms) as fixed factors. The lower bound of RT analysis was fixed at 200 ms to
308 ensure the validity and representativity of the observed behavior, because of the lack of
309 datapoints in 20 ms bins below this time (only 15 trials comprised between 180 ms and 200 ms
310 originating from 7 of the 22 participants). This might be explained by the shortest stimulus-
311 response interval fixed (100 ± 150 ms), allowing maximal RT of 250 ms. In this context, it was
312 optimal to wait as much as permitted to fully process the position and color associated with the
313 targets in order to reach the rewarded one, instead of initiating the movement too early and
314 missing the reward. The analysis (Success rates $\sim 1 + \text{Condition} + \text{RT} + \text{Condition}:\text{Sujet} + (1 +$
315 $\text{Condition} | \text{Sujet})$, $\text{AIC} = -3516.7$, $\text{BIC} = -2827.8$, $\text{marginal } R^2 = 0.31$, $\text{conditional } R^2 = 0.46$)
316 showed significant effects of Condition ($F(3,56.9) = 10.2$, $p = 10^{-5}$) and RT ($F(12,2481.0) =$
317 22.9 , $p < 10^{-5}$) on success rates and an interaction between Condition and RT ($F(36, 2481.1) =$
318 10.5 , $p < 10^{-5}$). Crucially, the difference in success rates between CONG and INCONG trials

319 was significant until the RT reached [340;360ms] ([200;220ms]: $t(108.8) = 10.6$, mean diff =
320 41.5%, $p < 10^{-5}$; [220;240ms]: $t(57.9) = 9.7$, mean diff = 32.2%, $p < 10^{-5}$; [240;260ms]: $t(51.9)$
321 = 6.9, mean diff = 22.5%, $p < 10^{-5}$; [260;280ms]: $t(51.9) = 5.8$, mean diff = 18.8%, $p = 10^{-4}$;
322 [280;300ms]: $t(51.9) = 4.2$, mean diff = 13.5%, $p = 0.002$; [300;320ms]: $t(51.9) = 3.2$, mean
323 diff = 10.9%, $p = 0.018$; [320;340ms]: $t(51.9) = 3.2$, mean diff = 10.5%, $p = 0.027$;
324 [340;460ms]: $t < 2.6$, mean diff $< 8.4\%$, $p > 0.160$).

325 Another way of assessing the difference in the accuracy of choices between CONG and
326 INCONG conditions is to use an absolute value of success rate (95%) as a criterion. 95%
327 confidence intervals (ci95) around the mean of success rates for each range of RT included the
328 value 95 as early as the lowest range of RT in the CONG condition ([200;220ms], mean =
329 94.4%, ci95 = [90.7;98.2]), whereas in the INCONG condition participants did not reach this
330 success rate until RTs of 350 ms ([340;360ms], mean = 91.4%, ci95 = [85.4;97.4]). This
331 observation is consistent with the previous results using GLMM. Overall, these results show
332 that participants needed an additional delay of approximately 150 (140 to 160) ms to achieve a
333 similar success rate when the high-cost target was rewarded compared to when the low-cost
334 target was rewarded, suggesting considerable interference of motor costs on reward-based
335 choices.

336 Critically, this difference in success rates between CONG and INCONG conditions was
337 not explained by a difference between trajectories needed to reach the LC and the HC target.
338 Indeed, there was no significant difference between R-HC and R-LC in success rates at any RT
339 tested ([200;460ms]: $t < 2.1$, mean diff $< 7.9\text{ms}$, $p > 0.530$). Additionally, the choice bias
340 observed in the INCONG condition did not appear to result from a default movement, made
341 without considering the presented targets at short RT, because we noted a significant difference
342 in success rates between INCONG and R-HC over RT ranging from 200 to 340 ms, comparable
343 to the difference previously found between CONG and INCONG conditions ([200;220ms]:

344 $t(169.1) = 7.2$, mean diff = 32.3 ms, $p < 10^{-5}$; [220;240ms]: $t(61.2) = 10.5$, mean diff = 36.3 ms,
345 $p < 10^{-5}$; [240;260ms]: $t(50.7) = 7.4$, mean diff = 24.2 ms, $p < 10^{-5}$; [260;280ms]: $t(50.1) = 6.1$,
346 mean diff = 19.9 ms, $p = 10^{-5}$; [280;300ms]: $t(50.1) = 4.5$, mean diff = 14.7 ms, $p = 10^{-4}$;
347 [300;320ms]: $t(50.1) = 3.7$, mean diff = 12.2 ms, $p = 0.007$; [320;340ms]: $t(50.1) = 3.6$, mean
348 diff = 11.6 ms, $p = 0.011$) until [340;360ms] ([340;460ms]: $t < 2.7$, mean diff < 8.7 ms, $p >$
349 0.156). This suggests that the shift in the initial trajectory observed in the INCONG condition
350 was specifically due to the presence of the non-rewarded LC target (Figure 3C). The difference
351 in initial choices between INCONG and R-HC conditions was also observable in the average
352 angle of the initial trajectory at shortest RT (Figure 4B).

353 The next question we asked was whether this bias in initial choice was further corrected
354 or not. We compared initial and final choices of participants in INCONG trials across RT
355 ranges. The GLMM included 2 fixed factors: Choice (2 levels: Initial and Final) and RT (13
356 levels: 20ms-bins ranging from 200 to 460ms). The selected model (Success rates $\sim 1 + \text{Choice}$
357 $+ \text{RT} + \text{Choice:RT} + (1 + \text{Choice} + \text{RT} \mid \text{Subject})$, AIC = -621.5, BIC = 206.5, marginal $R^2 =$
358 0.19, conditional $R^2 = 0.60$) demonstrated a significant effect of RT ($F(12,30.1) = 9.2$, $p < 10^{-5}$)
359 and a significant effect of Choice ($F(1,96.4) = 6.7$, $p = 0.01$) but no interaction between RT
360 and Choice ($F(12,1226.2) = 1.0$, $p = 0.441$). The magnitude of the Choice effect was relatively
361 low because success rates were only on average 2.6% [ci95: 0.7%;4.5%] higher in final choices
362 compared to initial choices. Additionally, the absence of interaction between Choice and RT
363 suggests that initial and final choices evolved in a similar manner as a function to RT.
364 Consequently, at shorter latencies participants' initial choices were not only biased in the
365 quadrant of the low-cost target, but their final choice also corresponded more often to the non-
366 rewarded target. This tendency was confirmed by the analysis conducted on the total earned
367 points. We first removed the MT-based correction (no decrease in the number of earned points
368 according to MT) so that the total amount of points was not influenced by the longer MT needed

369 to reach to the rewarded target in INCONG than in INCONG conditions (Figure 2A). The
370 analysis showed that participants won significantly more points in the CONG than in the
371 INCONG trials ($t(21) = 6.4$, mean diff = 42.3, $p < 10^{-5}$, Cohen's $d = 1.4$; Figure 3D). Hence,
372 the difference in motor costs between targets meaningfully impacted the total earnings of
373 participants.

374

375 **[Insert Figure 3]**

376

377 Beside motor costs, other factors might have also biased choices in the present task.
378 Namely, low-level visuo-attentional processes may also have had an influence. These
379 preferences possibly involve a right-hemifield visual bias for right-handed individuals as well
380 as for movements performed with the right hand (Coelho et al, 2013, Le et al, 2014). In order
381 to test for such visuo-attentional bias, we analyzed the difference in success rates between
382 CONG and INCONG conditions separately for each configuration of targets. We included only
383 trials with $RT < 350$ ms because it was at these latencies that motor costs significantly influenced
384 participants' choices in previous analyses (see above). The GLMM included Congruence
385 (CONG, INCONG) and Configuration (CONF1, CONF2, CONF3, CONF4) as fixed factors
386 (Success rates $\sim 1 + \text{Congruence} + \text{Configuration} + \text{Congruence:Configuration} + (1 +$
387 $\text{Congruence} + \text{Configuration} \mid \text{Subject})$, AIC = -766.3, marginal $R^2 = 0.23$, conditional $R^2 =$
388 0.62). It demonstrated a significant effect of Congruence ($F(1,21.1) = 28.6$, $p = 10^{-5}$),
389 Configuration ($F(3,26.3) = 5.1$, $p = 0.007$) as well as an interaction ($F(3,457.0) = 5.6$, $p = 0.001$).
390 Post-hoc analyses revealed significant differences in success rates between CONG and
391 INCONG for CONF1 ($t(35.7) = 5.0$, mean diff = 15.8%, $p = 10^{-5}$), CONF2 ($t(35.7) = 6.1$, mean
392 diff = 19.3%, $p < 10^{-5}$) and CONF4 ($t(35.7) = 4.6$, mean diff = 14.6%, $p = 10^{-4}$). This effect was

393 also significant for CONF3 but was of smaller magnitude ($t(35.7) = 2.9$, mean diff = 9.3%, $p =$
394 0.02; Figure 4A). This smaller effect for CONF3 suggests that a rightward visual bias could
395 have countered the influence of motor costs, because in this condition the LC target was located
396 on the left hemifield whereas the HC target was located on the right hemifield. Comparisons
397 between configurations of targets showed no significant difference in success rates in CONG
398 condition ($t < 0.5$, mean diff < 1.3 , $p = 1$), whereas success rates in INCONG were higher in
399 CONF3 compared to CONF1 ($t(46.8) = 3.0$, mean diff = 6.5%, $p = 0.024$) and CONF2
400 ($t(43.8) = 5.1$, mean diff = 11.3%, $p = 10^{-5}$). Hence, choices in INCONG condition were not
401 equivalent between configurations of targets, especially comparing CONF2 and CONF3.
402 Importantly, only the position of the HC target differed between both conditions (Figure 1C),
403 suggesting that this behavioral effect should be attributable to a different degree of preference
404 for HC targets depending on their locations. Indeed, the choice was significantly more biased
405 toward the LC target when the HC target was located in the upper left quadrant (CONF1 and
406 CONF2) compared to when it was located in the lower right quadrant (CONF3 and CONF4)
407 (Figure 4B). Overall, these results suggest that a rightward visual bias could have influenced
408 initial choices along with motor costs. Nonetheless, the lack of significant preference for the
409 LC target in CONF1 as compared to other target configurations limits this interpretation. Hence,
410 the existence of an early visual bias remains to be clarified.

411

412 **[Insert Figure 4]**

413

414 Finally, the last part of the analysis aimed to determine if motor costs were learned and
415 thus had a growing influence on participants' choices over the course of the experiment, or if
416 they consisted in a bias that was already present at the beginning of the experiment. The GLMM

417 included two fixed factors: Congruence (2 levels: CONG and INCONG) and Block (6 levels).
418 The analysis (Success rates $\sim 1 + \text{Congruence} + \text{Block} + (1 + \text{Congruence} | \text{Subject})$, AIC = -
419 1067.7, BIC = -915.2, marginal $R^2 = 0.16$, conditional $R^2 = 0.44$) revealed a significant effect
420 of Congruence on participants' choices ($F(1,20.9) = 23.9$, $p = 10^{-5}$) but neither a significant
421 effect of Block ($F(5,866.1) = 0.8$, $p = 0.544$) nor an interaction between Congruence and Block
422 ($F(5,866.1) = 1.2$, $p = 0.298$). The presence of a bias in choices between CONG and INCONG
423 as early as the first block and the absence of a significant change in this bias across blocks
424 suggest that the influence of motor costs on behavior was not acquired during the experiment.
425

426 DISCUSSION

427 This study revealed that varying the relative positions of targets, and thus the motor
428 costs associated with each movement, is enough to influence a decision based on simple visual
429 cues specifying rewards. Precisely, motor costs significantly biased initial choices, represented
430 by the direction of the hand trajectory 100 ms after movement onset, when RT ranged from 200
431 to 350 ms. This bias seemed to delay the normativity of the decision because it took
432 approximately 150 ms more to achieve a similar success rate when the rewarded target was the
433 most biomechanically costly (INCONG) compared to when the rewarded target carried the
434 lowest cost (CONG). Motor costs had a substantial impact since participants earned
435 significantly less reward in the INCONG than in the CONG condition. Importantly, the bias in
436 INCONG initial trajectory could not be explained as an intrinsic feature of the trajectory used
437 to reach the high-cost targets, since this deviation was not observed in one-target trials involving
438 a high-cost rewarded target (R-HC).

439 These results should be interpreted keeping in mind that reward information was varied
440 in the simplest way in our task with a binary color-based choice (see Materials & Methods for
441 details). The stimuli were equiluminant, there was no perceptual ambiguity between them, and
442 the perceptual evidence remained constant throughout the trial. Additionally, participants were
443 not explicitly informed that some targets would be easier to reach than others; they were only
444 told that green targets were associated with points and that whatever monetary gain they
445 accumulated by the end of the experiment would be theirs. A “normative” decision in this task
446 should thus only consider expected rewards and not motor costs since the latter were irrelevant
447 to the task. In this light, the fact that motor costs impacted time-constrained choices (impeding
448 success rates), speaks to the automatic nature of their influence. This extends previous studies
449 reporting a significant influence of motor costs on effort- (Cos et al, 2014; Morel et al, 2017;

450 Gallivan et al, 2017) and perceptual-based decision-making (Hagura et al, 2017; Marcos et al,
451 2015). This influence is particularly relevant to underline because the trajectory of reaching
452 movements has been frequently used to infer choices based on visual and cognitive information
453 (for reviews: Song & Nakayama, 2009; Gallivan et al, 2018) even in high-speed decision
454 contexts (Chapman et al, 2010, 2015; Carroll et al, 2019) but little interest has been given to
455 the impact of motor costs carried by the different targets in these contexts.

456 There is a debate between serial and parallel models regarding the functional
457 architecture underlying decision-making (Wispirski et al, 2020). In short, serial models state
458 that decisions are made in a space of goods representing abstract values of options in the
459 prefrontal cortex (Padoa-Schioppa et al, 2011), whereas parallel models suggest that decisions
460 are made in a space of actions through a competition between sensorimotor representations of
461 actions in parieto-frontal regions (Cisek & Kalaska, 2010). This debate is a central issue in the
462 understanding of the integration of motor costs in the decision process because there is evidence
463 that motor costs might be integrated with reward information in the prefrontal cortex (Cai &
464 Padoa-Schioppa, 2019), but also that they might bias the decision quickly and thus be rather
465 integrated in sensorimotor regions (Cos et al, 2014; Gallivan et al, 2017; Christopoulos et al,
466 2015). The present results do not allow to resolve this debate, because they can be explained by
467 both models. Indeed, in our task the success rate was not significantly different from 50% in
468 the INCONG condition at the shortest RTs (Figure 3C), meaning that participants might have
469 considered both reward and motor cost information before initiating their movements.
470 Consequently, motor costs could have increased the conflict in a competition between target
471 values, or conversely, they could have biased action representations while being modulated by
472 top-down signals specifying reward information. Nonetheless, the present study highlights the
473 importance of considering basic motor costs inherent to reaching in different directions, even
474 in a context in which target choices supposedly rely on other variables.

475 Previous studies have shown that motor costs influence decisions in less than 200 ms
476 (Cos et al, 2014), with activation of sensorimotor regions related to the evaluation of motor
477 costs found as early as 100 ms after stimulus onset (Harris & Lim, 2016). These data, in line
478 with ours, suggest that there appears to be no RT that is too fast for motor costs *not* to be
479 considered. This would be consistent with the rapid formation of sensorimotor representations
480 of action possibilities (Cisek & Kalaska, 2010), and point to the possibility that motor costs
481 might bias action representations at a very early stage. More specifically, reaching movements
482 are thought to be represented within directionally-tuned neuronal assemblies in the dorsal
483 parieto-frontal cortex, as a result of the integration of arm- and target-related sensory signals
484 (Buneo et al, 2002; Pesaran et al, 2006; Bernier et al, 2017). An intriguing possibility is that
485 motor costs are intrinsically factored in this arm-target integration process. This could take the
486 form of a gain on the activity of directionally-selective neurons when the reach direction incurs
487 low motor costs. Such “native” biasing of action representations according to cost may be akin
488 to a subset of these regions responding preferentially to targets in peripersonal space (i.e., at a
489 reachable distance) (Gallivan et al, 2009; 2011). This early bias has been suggested for
490 attentional and other cognitive biases in perception, under the concept of priority maps
491 (Andersen & Cui, 2009; Klink et al, 2014; Roggeman et al, 2010). A unifying mechanism
492 underlying visuo-attentional preferences and the influence of motor costs would also explain
493 why they both influenced choices at the shortest RTs in our task. Indeed, participants were more
494 accurate when the rewarded high-cost target was located in the right visual hemifield as
495 compared to when it was located in the left hemifield (see Figure 4B). This observation is
496 consistent with previous studies that demonstrated an ipsilateral hemifield preference for
497 movements performed with a given hand (Coelho et al, 2013; Le et al, 2014). Still, the motor
498 cost bias remained significant in all tested configurations of targets, suggesting that it was
499 robust in our task.

500 Alternatively, motor costs might be computed in other cortical and subcortical regions
501 that influence parieto-frontal activity. It may arise from inputs from the basal ganglia and the
502 cerebellum, which are known to modulate activity in sensorimotor regions by means of cortico-
503 subcortical loops (Pezzulo & Cisek, 2016). Previous studies suggested that motor costs could
504 influence action selection by the re-activation of a stored internal model of limbs biomechanics
505 in the cerebellum (Dounskaia et al, 2005; Goble et al, 2007). This is consistent with the
506 proposed role of the cerebellum in motor learning and prediction of sensory consequences of
507 movement (Shadmehr & Krakauer, 2008). Additionally, recent studies highlighted the
508 involvement of cortico-striatal circuits in the evaluation of effort mediated by dopamine,
509 including the medial frontal cortex and the dorsal striatum (Kurniawan et al, 2010; Prévost et
510 al, 2010; Zénon et al, 2015; Klein-Flugge et al, 2016). However, the role of dopamine in effort
511 encoding is currently a debated topic (Salamone et al, 2016; Walton & Bouret, 2018), and the
512 extent to which our results are linked to these preceding studies remains to be determined.
513 Indeed, most of them have used hand grip tasks in which participants had to assess the cost
514 associated with each level of isometric contraction and compare it with an expected reward by
515 means of explicit, conscious computations (Prévost et al, 2010; Zénon et al, 2015; Klein-Flugge
516 et al, 2016; Chen et al, 2020). This is in contrast with our task where motor costs inherent to
517 reaching movements are arguably assessed more implicitly, notably due to the absence of a
518 stimulus indicating the level of required effort. Moreover, varying the force or duration of an
519 isometric contraction results in only manipulating the energetic cost of the movement, whereas
520 the biomechanical preference for reaching in specific directions appears mainly driven by a
521 simplification of neural control (Goble et al, 2007). It constitutes a notable consideration
522 because motor costs are defined as a combination of an energetic cost and a control cost
523 (Shadmehr & Krakauer, 2008), and the perception of effort appears not to rely only on the
524 computation of an energetic cost (Morel et al, 2017).

525 One limitation concerning the interpretation of the results is a potential pre-existing
526 influence of motor costs on action selection, before processing target information. This concern
527 is related to previous studies that have shown that movements are biased toward the lowest cost
528 directions in a context where there is no target to reach (Wang & Dounskaia, 2012) or
529 movements have to be initiated before target onset (Haith et al, 2016). Consequently, an
530 alternative explanation of the rapid motor cost influence observed in the present results is that
531 this influence pre-existed the processing of target, and thus was independent of the position of
532 the presented targets. However, this pre-existing bias appears unlikely in our task for several
533 reasons. First, if this initial bias was pre-existing, we should have seen it also in the one-target
534 trials directed toward the high-cost target at the same RT. However, as detailed in the Results
535 section, there was no such bias. Second, if the bias was pre-existing, there should be movements
536 initiated in a quadrant where no target was displayed. However, there were very few of those
537 (0.3% of the trials, see Materials & Methods). Furthermore, it should be noted that we used four
538 different configurations of targets and alternated randomly two-target and one-target trials to
539 ensure stochasticity. In this context, participants could not anticipate where the targets would
540 appear, restricting their capacity to pre-plan their movements. Finally, participants appeared to
541 wait as much as permitted before initiating their movements (few trials with $RT < 200$ ms, see
542 Results), indirectly suggesting that they tried to process target information.

543 In conclusion, our results suggest that motor costs bias action selection even in a reward-
544 based decision-making context, possibly by providing an early boost to action representations
545 associated with lower motor costs. Consequently, when reward information is incongruent with
546 motor costs, this initial bias would have to be overcome by the gradual accumulation of
547 evidence in favor of the other rewarded action, thus accounting for the observed 150 ms delay.
548 This increasing (albeit slower) consideration of the associated reward is likely to be due to top-
549 down signaling from prefrontal cortex and basal ganglia, regions known to be involved in the

550 computation of stimulus-reward association rules (Sleezer et al, 2016; Ebitz et al, 2020).
551 Overall, these findings are in line with the perspective of a hierarchical influence of different
552 decisional variables on action representations, based on their level of abstraction (Cisek, 2012;
553 Pezzulo & Cisek, 2016). This underlines the importance of taking motor costs into
554 consideration when using dynamic motor tasks for studying decision-making and to further
555 investigate the underlying neural basis of the integration of motor costs in the action selection
556 process.
557

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- 711

712 **Figure legends**

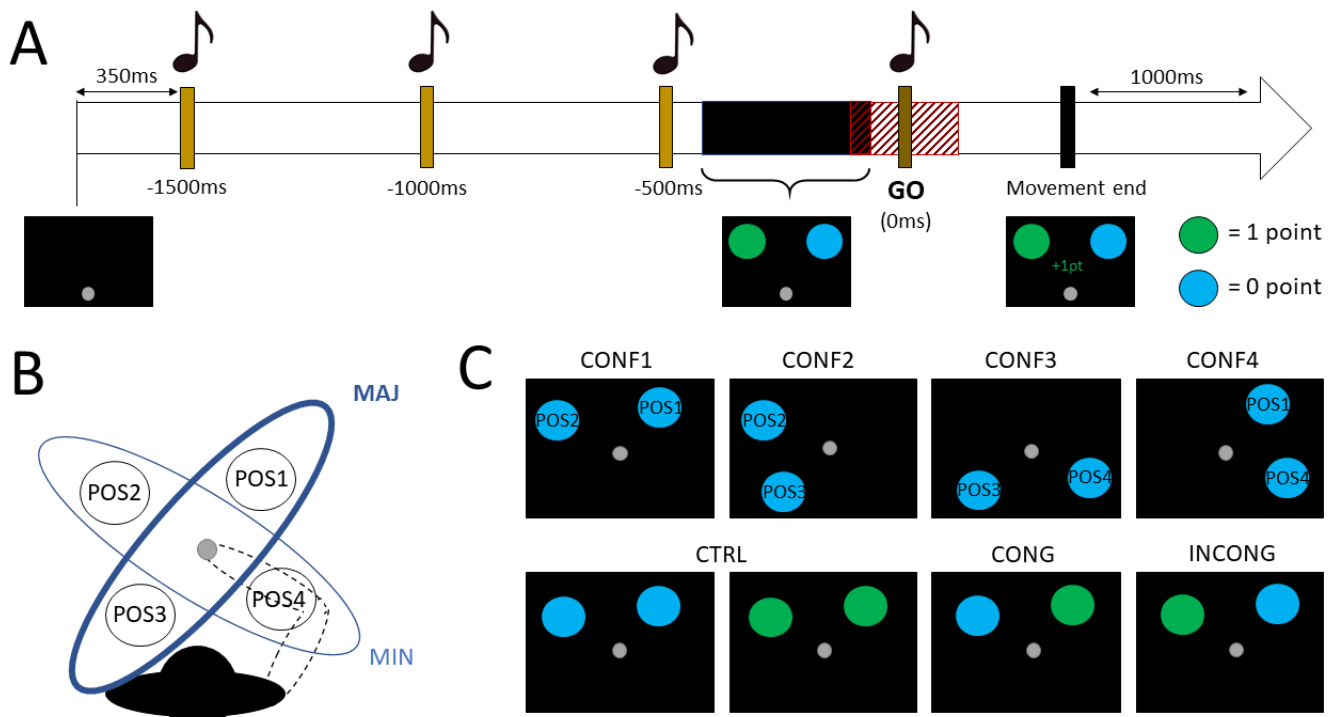
713 **Figure 1. Experimental design.** A: brown bars and musical notes indicate the four auditory
714 cues. The black horizontal bar indicates the range of target onsets (-400ms to -100ms before go
715 cue). The shaded red area around the go cue indicates valid movement onset interval (-150ms
716 to 150ms). Reported times under the brown bars correspond to time differences from go cue
717 (fourth tone). B: low-cost (LC) targets on positions 1 (POS1 = 60°) and 3 (POS3 = 240°) were
718 located on the major axis of the mobility ellipse (MAJ, thick blue ellipse) whereas high-cost
719 (HC) targets on positions 2 (POS2 = 150°) and 4 (POS4 = 330°) were located on the minor axis
720 of the mobility ellipse (MIN, thin blue ellipse). Dotted lines schematically illustrate the right
721 arm initial position, and the grey circle indicates the hand initial position. C: first row shows
722 the four configurations of targets used in the task. Second row illustrates the control (CTRL,
723 first and second panels), congruent (CONG, third panel) and incongruent (INCONG, fourth
724 panel) conditions for the first configuration of targets (CONF1).

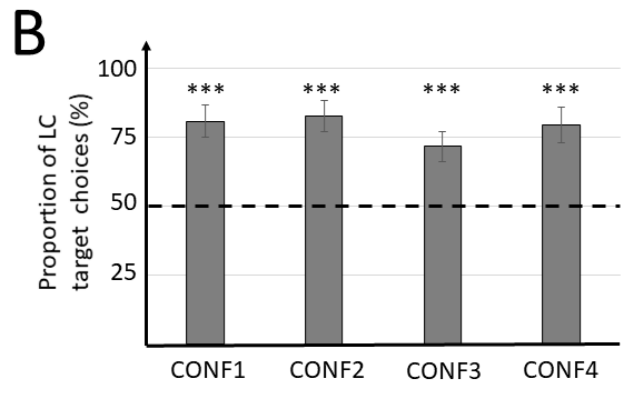
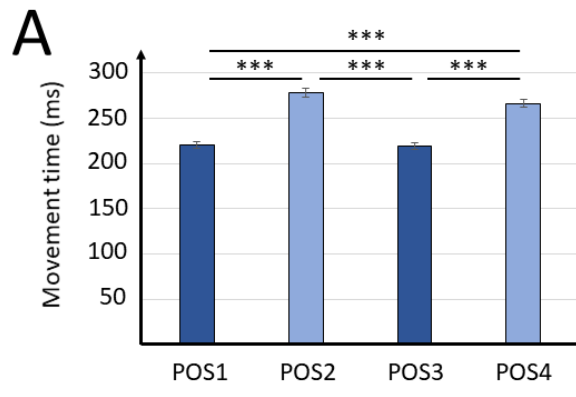
725 **Figure 2. Effects of motor costs on movements and choices without rewards.** A: average
726 MT for each target position in one-target trials. B: average proportion of LC target choices
727 (targets in positions 1 and 3), for each target configuration. Values higher than 50 demonstrate
728 a bias toward the LC target. Error bars indicate 95% confidence intervals around the mean.
729 * $p < .05$, ** $p < .01$, *** $p < .001$.

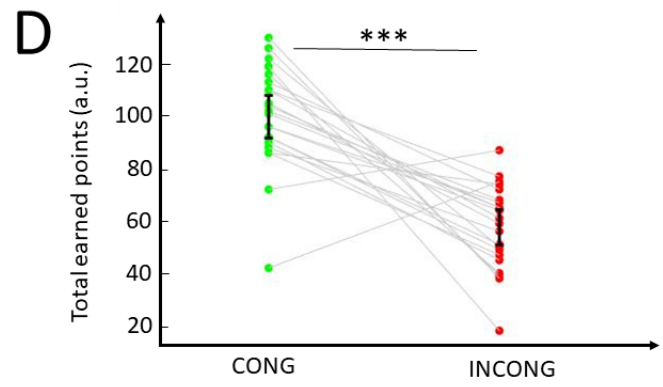
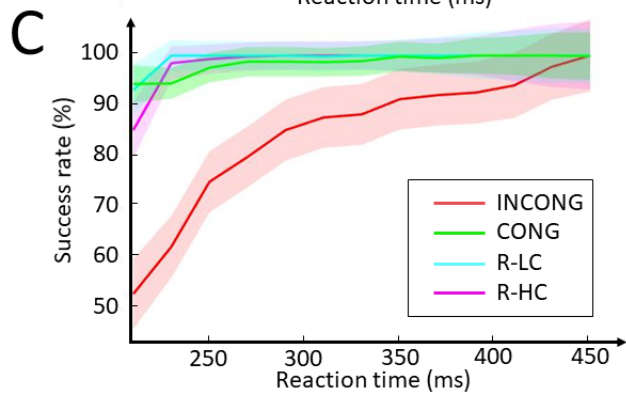
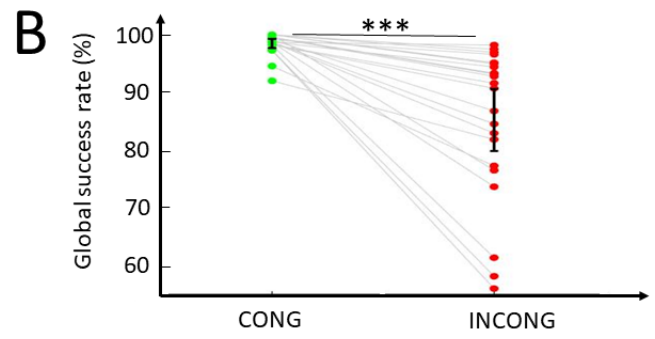
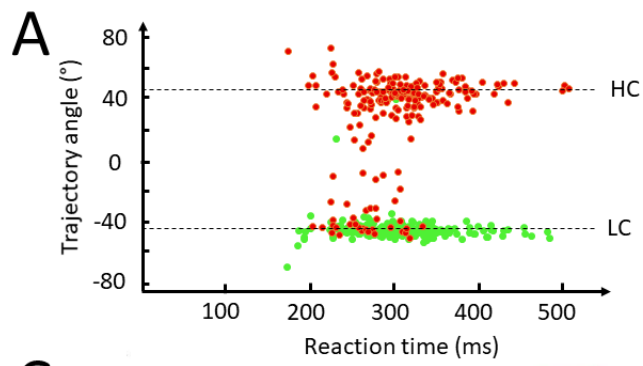
730 **Figure 3. Effects of motor costs on reward-based decision making.** A: distribution of
731 trajectory angles 100ms after movement onset as a function of RT in CONG (green dots) and
732 INCONG (red dots) conditions for a representative participant in CONF1. Dotted lines indicate
733 the angle of the low-cost (LC) target and high-cost (HC) targets. B: global success rates based
734 on initial choices (proportion of trials for which the hand location 100ms after movement onset
735 was in the quadrant of the rewarded target) in CONG and INCONG conditions for each

736 participant. C: success rates as a function of RT in CONG (green line), INCONG (red line), R-
737 LC (cyan line) and R-HC (magenta line) conditions. The shaded areas indicate 95% confidence
738 intervals around the mean. D: total earned points during the experiment in CONG and INCONG
739 conditions for each participant. Error bars indicate 95% confidence intervals around the mean.
740 * $p < .05$, ** $p < .01$, *** $p < .001$.

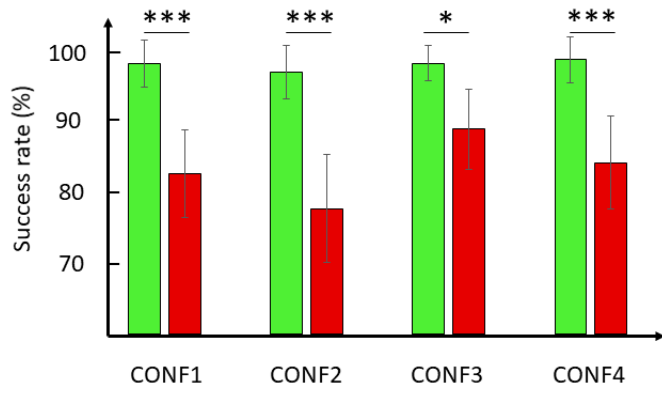
741 **Figure 4. Influence of target configuration on directional bias.** A: average success rates
742 according to configurations of targets and congruence (green bars=CONG, red bars=INCONG).
743 Error bars indicate 95% confidence intervals around the mean. ** $p < .01$, *** $p < .001$. B: mean
744 trajectory angle 100 ms after movement onset in INCONG condition for CONF1 (brown
745 arrows), CONF2 (red arrows), CONF3 (orange arrows), and CONF4 (yellow arrows), and in
746 R-HC condition for POS2 (dark purple arrows) and POS4 (light purple arrows). Concentric
747 circles indicate RT (grey values in ms).







A



B

