

1 **Title: Motor skill learning decreases motor variability and increases planning horizon**

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18 **Abstract**

19

20 We investigated motor skill learning using a path tracking task, where human subjects had to
21 track various curved paths at a constant speed while maintaining the cursor within the path
22 width. Subjects' accuracy increased with practice, even when tracking novel untrained paths.
23 Using a “searchlight” paradigm, where only a short segment of the path ahead of the cursor
24 was shown, we found that subjects with a higher tracking skill differed from the novice subjects
25 in two respects. First, they had lower motor variability, in agreement with previous findings.
26 Second, they took a longer section of the future path into account when performing the task,
27 i.e. had a longer planning horizon. We estimate that between one third and one half of the
28 performance increase was due to the increase in planning horizon. An optimal control model
29 with a fixed horizon (receding horizon control) that increases with tracking skill quantitatively
30 captured the subjects' movement behaviour. These findings demonstrate that human subjects
31 not only increase their motor acuity but also their planning horizon when acquiring a motor
32 skill.

33 **New and Noteworthy**

34 We show that when learning a motor skill humans are using information about the
35 environment from an increasingly longer amount of the movement path ahead to improve
36 performance. Crucial features of the behavioural performance can be captured by modelling
37 the behavioural data with a receding horizon optimal control model.

38 **Introduction**

39

40 The human motor system can acquire a remarkable array of motor skills. Informally, a person
41 is said to be “skilled” if he or she can perform faster and at the same time more accurate
42 movements than other, unskilled, individuals. What we don't know, however, is what learning
43 processes and components underlie our ability to move better and faster. One component may
44 be relatively “cognitive”, involving the faster and more appropriate selection and planning of
45 upcoming actions (Diedrichsen and Kornysheva 2015; Wong et al. 2015). Another component
46 may be related to motor execution – the ability to produce and fine control difficult
47 combinations of muscle activations (Shmuelof et al. 2012; Waters-Metenier et al. 2014).
48 Depending on the structure of the task, changes in visuo-motor processing or feedback control
49 may also contribute to skill development. Motor adaptation extensively studied using
50 visuomotor and force perturbations (Shadmehr et al. 2010), may play a certain role in
51 stabilizing performance, but it cannot by itself lead to improvements in the speed-accuracy
52 trade-off (Wolpert et al. 2011).

53

54 A task commonly used in the experiments on motor skill learning is sequential finger tapping,
55 where subjects are asked to repeat a certain tapping sequence as fast and as accurately as
56 possible (Karni et al. 1995, 1998; Petersen et al. 1998; Walker et al. 2002). Improvement in
57 such a task can continue over days, but previous papers have focussed mostly on the learning
58 that is specific to the trained sequence(s) (Karni et al. 1995).

59

60 Many real-world tasks, however, do not involve the production of a fixed sequence of motor
61 commands, but the flexible planning and execution of movements. Such flexibility is often well
62 described by optimal feedback control models (Braun et al. 2009; Diedrichsen et al. 2010;

63 Todorov and Jordan 2002) where the skilled actor appears to compute “on the fly” the most
64 appropriate motor command for the task at hand. This requires demanding computations
65 (Todorov and Jordan 2002), and the human motor system likely has found heuristics to deal
66 with this complexity. One way to reduce complexity of the control problem is to not optimize
67 the whole sequence of motor commands that will achieve the ultimate goal, but to only optimise
68 the current motor command for a short distance into the future. This idea is called receding
69 horizon control, also known as model predictive control (Kwon and Han 2005). Under this
70 control regime, the system computes a feedback control policy that is optimal for a finite
71 planning horizon. The control policy is then continuously updated as the movement goes on
72 and the planning horizon is being shifted forward. This allows for adaptability, e.g. it can
73 flexibly react to perturbations or unexpected challenges, as sensory information becomes
74 available. Recent studies provided indirect evidence that favour the optimisation of short time-
75 periods of a motor command (Dimitriou et al. 2013). The notion of planning horizon also arises
76 in reinforcement learning, e.g. in the context of the so-called successor representation
77 (Momennejad et al. 2017).

78

79 Motivated by these ideas, we propose that some of the skill of a down-hill skier or a race-car
80 driver may lie not only in the increased ability to execute difficult motor commands (e.g. due
81 to decreased motor variability), but also in the ability to plan further ahead and to optimize the
82 movements for a longer time period into the future. In addition, we propose that the time span
83 that subjects plan ahead increases with experience, leading to an increasing performance with
84 training.

85

86 To test this idea, we designed an experimental condition which would allow us to measure the
87 planning horizon that skilled actors are using when executing long sequence of movements that

88 need to be planned “on the fly” – i.e. where the actual sequence of movements cannot be
89 memorized. For this, we developed a path tracking task, where subjects had to maintain their
90 cursor within a path that was moving towards them at a fixed speed. A similar task has been
91 previously used in motor control research (Poulton 1974), using a mechanical apparatus with
92 paths drawn on a paper roll that was moving at a fixed speed. It has been shown that subjects
93 are able to increase their accuracy with training, but the different computational strategies
94 between expert subjects and naïve performers remain unclear. In our study we use ‘searchlight’
95 trials in which subjects see various lengths of the approaching path ahead of their cursor to
96 probe subjects forward planning and compare experts and novices in this respect.

97

98 **Materials and Methods**

99 **Subjects**

100 62 experimentally naïve subjects took part in this experiment (33 males and 29 females, age
101 range 20-52 years old). Subjects gave written informed consent and were paid 10 €/h. The
102 experimental procedures received ethics approval from the University of Freiburg.

103

104 **Setup**

105 Subjects sat at a desk looking at a computer monitor (Samsung Syncmaster 226BW) located
106 ~80cm away. A cursor displayed on the screen (Matlab and Psychophysics Toolbox Version 3
107 (Brainard 1997)) was under position control by movements of a computer mouse. The mouse
108 could be moved on the desk in all directions but only the horizontal (left and right) component
109 contributed to the cursor movement: the vertical position of the cursor was fixed at 5.7mm
110 above the base of the screen.

111

112 **Task**

113 To begin each trial subjects had to press the space bar. This displayed the cursor ($R=2.9\text{mm}$,
114 1.1cm from the bottom of the screen) and the path (width = 2.83cm) that extended from the top
115 to bottom of the screen (30cm). The path continuously moved downward on the screen at a
116 vertical speed of 34.1cm/s . The initially visible path was a straight line centered in the middle
117 of the screen with the cursor positioned in the middle of the path. Once this initial section
118 moved through the screen, the path then followed a random curvature (Fig. 1A). Subjects were
119 instructed to keep the cursor between the path borders at all times moving only in the horizontal
120 plane and were told to be as accurate as possible. The cursor and path were displayed in white

121 if the cursor was within the path and both turned red when it was outside the path, always on a
122 black background.

123

124 The cursor position was sampled at 60 Hz and the tracking accuracy was defined for each trial
125 as the percentage of time steps when the cursor was inside the path. Running accuracy values
126 were continuously displayed in the top left corner of the screen and final accuracies were
127 displayed between the trials.

128

129 This experiment is based on a previous version where subjects were asked to track static
130 randomly curved paths in 2D as quickly as possible without touching the sides [unpublished
131 data, (Bashford et al. 2014)]. We later found that the 1D paradigm presented here was better
132 suited to study the planning horizon as the speed was fixed.

133 **Paradigm**

134 Subjects were randomly assigned into two groups: expert (N=32) and naive (N=30). The
135 paradigm included a training (expert group only) and a testing (all subjects) phase. Subjects in
136 the expert group trained over 5 consecutive days, each day completing 30 minutes of path
137 tracking (10 of 3-minute trials with short breaks in-between, searchlight length (s) 100%). If
138 the performance improved from one trial to the next subjects saw a message saying
139 “Congratulations! You got better! Keep it up!”, otherwise the message “You were worse this
140 time! Try to beat your score!” was shown. The training paths were randomly generated on the
141 fly. Experts performed the testing set of trials after a short break following training on the final
142 (5th) day. Naïve subjects performed only the testing set of trials.

143

144 The testing phase lasted 30 min (30 of 1-minute trials with breaks in-between) using 30
145 different pre-generated paths that were the same for all subjects. The testing phase in this

146 experiment contained 3 normal trials (s=100%) and 27 searchlight trials (s=10-90%) where
147 some upper part of the path was not visible. Three blocks of 10 trials with the searchlight length
148 ranging from s=10% to s=100% (in steps of 10%) were presented, with the order shuffled in
149 each block; the same fixed pseudorandom sequence was used for all subjects.

150

151 **Path generation**

152 Paths were generated before each trial start during training and a pre-generated fixed set was
153 produced in the same way for testing. Each path was initialized to start at the bottom middle of
154 the screen and the initial 30 cm of each path were following a straight vertical line. Subsequent
155 points of the path midline had a fixed Y step of 40 pixels (1.1 cm) and random independent
156 and identically distributed (iid) X steps drawn from a uniform distribution from 1 to 80 pixels
157 (2.7mm – 2.2cm). Any step that would cause the path to go beyond the right or left screen
158 edges was recalculated. The midline was then smoothed with a Savitzky-Golay filter (12th
159 order, window size 41) and used to display path boundaries throughout the trial. All of the
160 above parameters were determined in pilot experiments to create paths which were very hard
161 but not impossible to complete after training.

162

163 **Statistical analysis**

164 In all cases, we used nonparametric rank-based statistical tests to avoid relying on the normality
165 assumption. In particular, we used Spearman's correlation coefficient instead of the Pearson's
166 coefficient, Wilcoxon signed-rank test instead of paired two-sample t-test, and Wilcoxon-
167 Mann-Whitney ranksum test instead of unpaired two-sample t-test.

168

169 We initially recorded N=10 subjects in each group and observed statistically significant
170 ($p < 0.05$) effect that we are reporting here: positive correlation between the asymptote
171 performance and the horizon length, as estimated via the changepoint and exponential models.
172 We then recorded another N=20/22 (naïve/expert) subjects per group to confirm this finding.
173 This internal replication confirmed the effect ($p < 0.05$). The final analysis reported in this study
174 was based on all N=62 subjects together. A preliminary version of the analysis for the initial
175 N=10/10 subjects can be found in our preprint (Bashford et al. 2014), but note that it used a
176 different way to estimate planning horizon compared to the procedure presented here, and so
177 the values are not directly comparable.

178

179 **Changepoint and Exponential model**

180 We used two alternative models to describe the relationship between the searchlight length and
181 the accuracy: a linear changepoint model and an exponential model. We used two different
182 models to increase the robustness of our analysis and both models support our conclusions.

183

184 The changepoint model is defined by

$$185 \quad y = \begin{cases} cs + o & \text{if } s \leq h_{cp} \\ ch_{cp} + o & \text{if } s > h_{cp} \end{cases}$$

186 where y is the subject's performance, s the searchlight length and (c, o, h_{cp}) are the subject-
187 specific parameters of the model which define the baseline performance at searchlight 0% (o),
188 the amount of increase of performance with increasing searchlight (c) and the planning horizon
189 (h_{cp}) after which the performance does not increase any further.

190

191 The exponential model is defined by

$$192 \quad y = \psi - \exp(-\rho s + d)$$

193 where the subject-specific parameters (ψ , d , ρ) specify the performance at searchlight 0% ($\psi -$
194 $\exp[d]$), the asymptote for large searchlights (ψ) and the speed of performance increase (ρ).
195 This function monotonically increases but it never plateaus. The speed of the increase depends
196 on the parameter ρ with larger values meaning faster approaching the asymptote. We used the
197 following quantity as a proxy for the “effective” planning horizon: $10 + \log(5)/\rho$. It can be
198 understood as the searchlight length that leads to performance being five times closer to the
199 asymptote than at $s=10\%$. The $\log(5)$ factor was chosen to yield horizon values of roughly the
200 same scale as with the changepoint model above.

201

202

203 Both models (changepoint and exponential) were fit to the raw performance data of each
204 subject, i.e. to the 30 data points, 3 for each of the 10 searchlight length values. The exponential
205 fit (see Equation 2 in the Results) was done with the Matlab's `nlinfit()` function, implementing
206 Levenberg-Marquardt nonlinear least squares algorithm. The changepoint fit (see Equation 1
207 in the Results) was done with a custom script that worked as follows. It tried all values of h_{cp}
208 on a grid that included $s=10\%$ and then went from $s=20\%$ to $s=100\%$ in 100 regular steps. For
209 each value of h_{cp} the other two parameters can be found via linear regression after replacing all
210 $s > h_{cp}$ values with h_{cp} . We then chose h_{cp} that led to the smallest squared error.

211

212 **Trajectory analysis**

213 To shed light on the learning process we analysed additional parameters of the subjects’
214 movement trajectories.

215 First, we computed the time lag between the subjects’ movement trajectories and the midline
216 of the paths (Figure 4A-B). To compute the lags, we interpolated both cursor trajectories and

217 path midlines 10-fold (to increase the resolution of our lag estimates). We computed the
218 Pearson correlation coefficient between cursor trajectory and path midline for time shifts from
219 of -300 to 300 ms, and defined the time lag as the time shift maximizing the correlation. Second,
220 we extracted the cursor trajectories in all sections across all paths that shared a similar curved
221 shape to explore the differences in cursor position at the apex of the curve (Figure 4C). The
222 segments were selected automatically by sliding a window of length 18 cm across the path. We
223 included all segments that were lying entirely to one side (left or right) of the point in the middle
224 of the sliding window ("C-shaped" segments), with the upper part and the lower part both going
225 at least 4.5 cm away in the lateral direction (see Figure 3). Our results were not sensitive to
226 modifying the exact inclusion criteria.

227 To draw the 75% coverage areas of the path inflection points in each group (Figure 4C), we
228 first performed a kernel density estimate of these points using the Matlab function `kde2d()`,
229 which implements an adaptive algorithm suggested in (Botev et al. 2010). After obtaining the
230 2d probability density function $p(x)$, we found the largest h such that $\int p(x)dx > 0.75$ over the
231 area where $p(x) > h$. We then used Matlab's `contour()` function to draw contour lines of height h
232 in the $p(x)$ function.

233

234 **Receding horizon model**

235 We modelled subjects' behaviour by a stochastic receding horizon model in discrete time t . In
236 receding horizon control (RHC, (Kwon and Han 2005)) motor commands u_t are computed to
237 minimize a cost function L_t over a finite time horizon of length h :

$$238 \quad \text{minimize } L_t(\{x_t\}, \{u_t\}) \quad (1)$$

$$239 \quad \text{subject to } L_t = \sum_{k=1}^h l_{t+k}$$

$$240 \quad x_{t+1} = f(x_t, u_t)$$

241 where f defines the dynamics of the controlled system. Equation (1) is equivalent to an optimal
242 control problem over the fixed future interval $[t + 1, t + h]$. Solving (1) yields a sequence of
243 optimal motor commands $\{u_0^{opt}, u_1^{opt}, \dots, u_{h-1}^{opt}\}$. The control applied at time t is the first
244 element of this sequence, i.e. $u_t = u_0^{opt}$. Then, the new state of the system x_{t+1} is measured
245 (or estimated) and the above optimization procedure is repeated, this time over the future
246 interval $[t + 2, t + 1 + h]$, starting from the state x_{t+1} .

247

248 Applying RHC to our experimental task, the dynamics of the cursor movement was modelled
249 by a linear first-order difference equation:

$$250 \quad x_{t+1} = x_t + u_{t-\tau} + \eta_t \quad \eta_t \in \mathcal{N}(0, \sigma^2) \quad (2)$$

251 where t is the time step, x_t the cursor position at time t , u_t is the motor command applied at
252 time t and τ the motor delay. η_t is the motor noise which was modelled as additive Gaussian
253 white noise with zero mean and variance σ^2 . We used the following cost function

$$254 \quad L_t = \sum_{k=\tau+1}^h [-\log(q_{t+k}) + \lambda |u_{t-\tau+k-1}|^2] \quad (3)$$

255 where L_t is the expected cost at time t , q_{t+k} is the probability of the cursor being inside the path
256 at time $t+k$, h is the length of the horizon in time and λ is the weight of the motor command
257 penalty. At every time step t , L_t is minimized to compute u_t while $\{u_0, \dots, u_{t-1}\}$ are known.
258 Consequently, the lower bound of the sum in (3) is $\tau + 1$. The cost function in (3) reflects a
259 trade-off between accuracy (first term, i.e. $\log[q_{t+k}]$) and effort (second term) whereas their
260 relative importance is controlled by λ . Cost functions with a similar accuracy-effort trade-off
261 have been used previously to successfully model human motor behaviour (Braun et al. 2009;
262 Diedrichsen 2007; Todorov and Jordan 2002).

263 We assume that subjects have acquired a forward model of the control problem and they can,
 264 therefore, predict the cursor position at time $t+1$ from the cursor position at time t and the motor
 265 command in accordance with equation (2). We also assume that subjects have an accurate
 266 estimate of the position of the cursor at time t , i.e. x_t is known. Subjects can then compute the
 267 probability distribution of the cursor position at future times $t+k$, given by:

$$268 \quad p(x_{t+k}|x_t, \{u_{t-\tau}, u_{t-\tau+1}, \dots, u_{t-\tau+k-1}\}) = \frac{1}{\sqrt{2\pi k\sigma^2}} e^{-\frac{(\hat{x}_{t+k})^2}{2k\sigma^2}} \quad (5)$$

269 with

$$270 \quad \hat{x}_{t+i} = x_t + \sum_{l=1}^i u_{t-\tau+l-1} \quad (6)$$

271 The probability of the cursor being inside the path is then given by

$$272 \quad q_{t+k} = \int_{m_{t+k}-\frac{w}{2}}^{m_{t+k}+\frac{w}{2}} \frac{1}{\sqrt{2\pi k\sigma^2}} e^{-\frac{(\hat{x}_{t+k}-z)^2}{2k\sigma^2}} dz \quad (7)$$

273 where m_t is the position of the midline of the path at time t and w the width of the path. The
 274 receding horizon model assumes that motor commands u_t are computed by minimizing the
 275 cost L_t in each time step t for a fixed and known set of model parameters $(h, \lambda, \tau, \sigma^2)$. We
 276 simplify the optimisation problem by approximating q_{t+k} by

$$277 \quad q_{t+k} \approx w \frac{1}{\sqrt{2\pi k\sigma^2}} e^{-\frac{(\hat{x}_{t+k}-m_{t+k})^2}{2k\sigma^2}} \quad (8)$$

278 The higher $k\sigma_k^2$ is relative to the path width w , the higher the accuracy of this approximation.
 279 Note that the squared error is scaled by $k\sigma^2$ and hence, errors in the future are discounted. This
 280 is a consequence of the used model of the cursor dynamics in (equation 2).

281 Using equation (8) and removing all terms which do not depend on u_t , we can derive a
 282 simplified cost function

$$283 \quad \tilde{L}_t = \sum_{k=\tau+1}^h \left[\frac{(\hat{x}_{t+k} - m_{t+k})^2}{2k\sigma^2} + \lambda |u_{t-\tau+k-1}|^2 \right] \quad (9)$$

284 Equation (9) shows that the trade-off between accuracy and the magnitude of the motor
 285 commands is controlled by $\sigma^2\lambda$. We therefore can eliminate one parameter and use the
 286 equivalent cost function

$$287 \quad \tilde{L}_t = \sum_{k=\tau+1}^h \left[\frac{(\hat{x}_{t+k} - m_{t+k})^2}{2k} + \tilde{\lambda} |u_{t-\tau+k-1}|^2 \right] \text{ with } \tilde{\lambda} = \sigma^2\lambda \quad (10)$$

288 The gradient of the cost function \tilde{L}_t is given by

$$289 \quad \frac{\partial \tilde{L}_t}{\partial u_{t+j}} = 2\tilde{\lambda}u_{t+j} + \sum_{k=j+(\tau+1)}^h \left[\frac{(\hat{x}_{t+k} - m_{t+k})}{k} \right] \quad (11)$$

290 with $j = 0, \dots, h - (\tau + 1)$. The Hessian of the cost function is given by

$$291 \quad \frac{\partial^2 \tilde{L}_t}{\partial u_{t+m} \partial u_{t+n}} = 2\delta_{m,n}\tilde{\lambda} + \sum_{k=\max(m,n)+(\tau+1)}^h \frac{1}{k} \quad (12)$$

292 with $m, n = 0, \dots, h - (\tau + 1)$. For $\tilde{\lambda} = 0$ all pivots of the Hessian matrix are positive and
 293 therefore the Hessian is positive definite for $\tilde{\lambda} = 0$. For the general case $\tilde{\lambda} > 0$ the Hessian
 294 remains positive definite as $H_2 = H_1 + D$ is positive definite if H_1 is positive definite and D is
 295 a diagonal matrix with only positive diagonal entries. Given the positive definiteness of the
 296 Hessian we can conclude that the cost function \tilde{L}_t is strictly convex with a unique global
 297 minimum. Setting the gradient (12) to $\mathbf{0}$ defines a system of $h-\tau$ linear equations with $h-\tau$
 298 unknowns $(u_t, \dots, u_{t+h-(\tau+1)})$ which solution minimizes \tilde{L}_t . The solution can be computed
 299 efficiently using standard numerical techniques. We used the ‘linsolve’ function of MATLAB
 300 (R2016b) which uses LU factorization.

301 As a measure of task performance, we computed the expected time inside the path from the
 302 model trajectory z_t as follows

$$303 \quad a = \frac{1}{T} \sum_{t=1}^T \left[1 - \int_{m_{t-\frac{w}{2}}}^{m_{t+\frac{w}{2}}} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(z_t-\eta)^2}{2\sigma^2}} d\eta \right] \quad (13)$$

304 with T depicting the number of time steps per path. The lag was computed by maximizing the
305 correlation coefficient between the model trajectories and the path midline identical to how the
306 lag was computed for the subjects' trajectories.

307 When applying the model to the searchlight path we made the additional assumption that the
308 model horizon increases with searchlight length s up to a maximal value h_{max} beyond which
309 the model horizon remains constant:

$$311 \quad h(s) = \begin{cases} s, & s < h_{max} \\ h_{max}, & s \geq h_{max} \end{cases} \quad (14)$$

310

312 **Fitting the receding horizon model to subjects' behaviour**

313 We fitted the RHC model to the subjects' movement trajectories in the searchlight testing paths
314 using Bayesian inference (Gelman et al. 2003). The model parameters were estimated by
315 computing their expected values from the posterior distribution

$$316 \quad \hat{\beta} = \langle \beta \rangle = \int \beta p(\beta|v) d\beta \quad (15)$$

317 where β is the model parameter, v the movement trajectory data of a subject and $p(\beta|v)$ the
318 posterior probability distribution for β . We approximated the integral in (15) by sampling from
319 the posterior distribution using the Metropolis algorithm which can sample from a target
320 distribution that can be computed up to a normalizing constant (Gelman et al. 2003). The RHC
321 model has four parameters $(h_{max}, \tau, \tilde{\lambda}, \sigma^2)$ out of which three $(h_{max}, \tau, \tilde{\lambda})$ affect the shape of
322 the trajectory (cf. equation (10)). Assuming a flat prior for the model parameters, i.e. $p(h_{max}, \tau, \tilde{\lambda}) = \text{const.}$, and a non-informative prior for the error-variance δ^2 , i.e. $p(\delta^2) = 1/\delta^2$
323 (Gelman et al. 2003), we obtained the following equation for the posterior

$$325 \quad p(\beta|w) \propto p(h_{max}, \tau, \tilde{\lambda}) \frac{1}{\delta^{2+N}} e^{-\frac{\text{mse}(h_{max}, \tau, \tilde{\lambda})}{2\delta^2}} \quad (16)$$

326 where $mse(h_{max}, \tau, \tilde{\lambda})$ is the mean squared error between the model and the subject movement
 327 trajectories and N the number of trials. The mean squared error between the movement
 328 trajectories of a subject and the model is given by

$$329 \quad mse(h_{max}, \tau, \tilde{\lambda}) = \frac{1}{10T|\mathcal{F}|} \sum_{s=1}^{10} \sum_{j \in \mathcal{F}_s} \sum_{t=1}^T \left(v_t^{(s,j)} - z_t^{(s,j)}(h_{max}, \tau, \tilde{\lambda}) \right)^2 \quad (17)$$

330 with T depicting the number of time steps per path, \mathcal{F}_s the set of paths ids for searchlight s ,
 331 $v_t^{(s,j)}$ the movement of subject i at time t in path j for searchlight s and $z_t^{(s,j)}(h_{max}, \tau, \tilde{\lambda})$ the
 332 corresponding movement predicted by the RHC model.

333 To save computation time, we precomputed the mse for specific discrete combinations of the
 334 model parameters. The model horizon parameter h_{max} could take any integer value between 1
 335 and 26 given a maximum possible planning horizon of 30cm (vertical screen size) which is
 336 equivalent to $30\text{cm} / \left(34 \frac{\text{cm}}{\text{s}} \cdot \frac{1}{30} \text{s} \right) = 30\text{cm} / \left(\frac{34}{30} \text{cm} \right) \approx 26$ time steps, where 34 cm/s is the
 337 path speed and 1/30s the time step. Hence, admissible values for the horizon parameter
 338 corresponded to horizons of $h_{max} = (1, \dots, 26) * \frac{34}{30} \text{cm}$. For the delay we allowed the values
 339 $\tau = (1, \dots, 15) * \frac{1}{30} \text{s}$, assuming that subjects won't have larger delays than 500ms. In fact, the
 340 maximum delay of a subject we found from fitting was 286 ms which is well below the limit
 341 we imposed. The motor penalty parameter $\tilde{\lambda}$ was allowed to take any of 10^3 logarithmically
 342 equally spaced values between 10^{-4} and 10^7 and 0. In total, we had, therefore,
 343 $26 \times 15 \times 1001 = 390390$ admissible parameter combinations for h_{max}, τ and $\tilde{\lambda}$. We simulated the
 344 model for all of these parameter values and computed the mean squared errors according to
 345 equation (17). We then used the Metropolis algorithm to generate 10^6 samples from the
 346 posterior distribution of the parameters. Each sample consisted of a 4-tuple of values for the
 347 parameters $(h_{max}, \tau, \tilde{\lambda}, \delta^2)$. We computed the motor noise parameter of the model σ^2 from the

348 estimated error-variance δ^2 as explained below and then $\lambda = \tilde{\lambda}/\sigma^2$ (cf. equation 10). For each
349 parameter sample we also computed the lag, as explained at the end of the previous section,
350 and the task performance using equation (13). As a result, we obtained 10^6 parameter values,
351 lags and task performances, which reflect samples from the posterior distribution of the model
352 parameters.

353 To evaluate the quality of the model, we used three-fold cross-validation where in each fold
354 the posterior distributions of the model parameters were estimated using the data from two of
355 the three trials for each searchlight. The posterior distributions were then used to make model
356 predictions of performance and lag in the remaining trial for each searchlight. This was done
357 for each subject separately and the model predictions were compared to the experimentally
358 observed performances and lags (cf. Fig. 5A-D).

359 Expected values of the model parameters were computed according to equation (13). Expected
360 values were calculated for each cross-validation fold separately and then averaged across the
361 three cross-validation folds. This yielded the model parameters $h_{max}, \tau, \lambda, \sigma^2$ for each subject,
362 shown in Fig. 5E-H.

363

364 *Estimation of the motor noise parameter from the error-variance*

365 If all model assumptions are fulfilled, the motor noise model parameter σ^2 will be linearly
366 related to the error-variance δ^2 and we should therefore be able to estimate σ^2 from δ^2 . For
367 each subject we computed σ^2 by minimizing the squared error between the model task
368 performance (eq. 13) and the experimentally determined task performance. A scatter plot of
369 the resulting σ^2 over the error-variance δ^2 revealed an approximate linear relationship between
370 σ^2 and δ^2 . We then determined the proportionality factor α by linear-least squares regression
371 of the model $\sigma^2 = \alpha\delta^2$ and used it to compute σ^2 from δ^2 . The linear-least squares regression

372 was done for each subject separately, using only the σ^2 and δ^2 values from all other subjects
373 to avoid overfitting.

374

375 **Estimating the influence of model parameters on performance difference between expert** 376 **and naïve groups**

377 To estimate how much a single model parameter causes the experts' gain in performance we
378 computed the performance of the model for naïve group parameters but with one parameter
379 (horizon, motor noise, delay or motor penalty) changed to expert group values. We also
380 performed the opposite procedure, replacing each parameter for each participants of the expert
381 with those of the naïve group. Using the Bayesian inference approach described in the previous
382 section, we replaced the full posterior distribution of the affected parameter with the posterior
383 distribution from the other group. This procedure was carried out for each subject separately
384 and the posterior of the affected parameter was replaced by the posterior of each subject from
385 the other group separately. We then computed the posterior of the performance curve and from
386 that the expected values of the performance by averaging. Hence, we obtained for each
387 parameter change $N_e \cdot N_n$ performance curves where N_e and N_n are the number of subjects in the
388 expert and naïve group, respectively. These performance curves were averaged and compared
389 to the average performances for the expert and naïve groups obtained for the fitted model (see
390 Results for details).

391

392 Parts of the modelling computations were run on the high-performance computing cluster
393 NEMO of the University of Freiburg (<http://nemo.uni-freiburg.de>) using Broadwell E5-2630v4
394 2.2 GHz CPUs.

395 All analysis code is available at <https://github.com/dkobak/path-tracking>.

396

397 Results

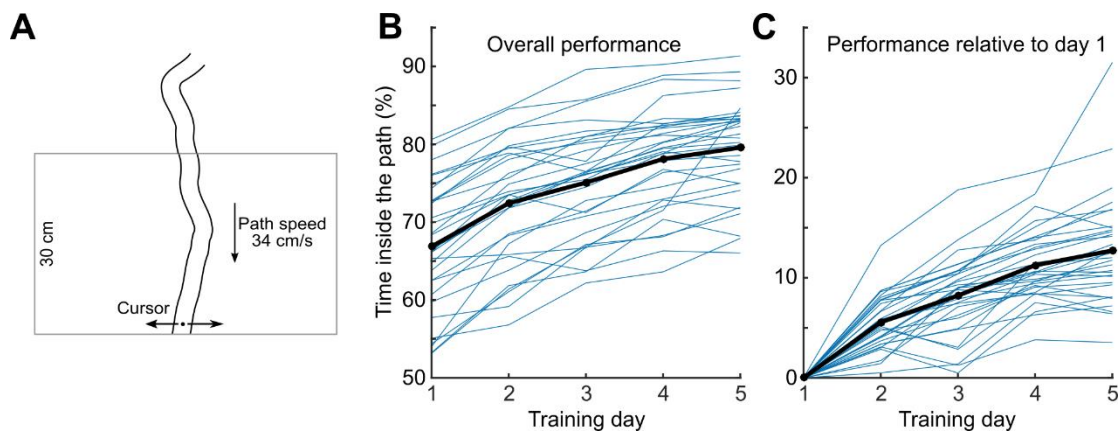
398

399 Learning the Tracking Skill

400 We designed an experiment where subjects had to track a path moving towards them at a
401 fixed speed (Fig. 1A and Methods). The narrow and wiggly path was moving downwards on a
402 computer screen while the cursor had a fixed vertical position in the bottom of the screen and
403 could only be moved left or right. Accuracy, our performance measure, was defined as the
404 fraction of time that the cursor spent inside the path boundaries. One group of subjects (the
405 expert group, N=32) trained this task for 30 minutes on each of 5 consecutive days. Another
406 group (the naïve group, N=30) did not have any training at all. Both groups then performed a
407 testing block that we describe below.

408

409



410

411 *Figure 1. Experimental Paradigm. (A) Subjects had to track a curved path that was dropping*
412 *down from top to bottom of the screen with a fixed speed of 34 cm/sec by moving the cursor*
413 *horizontally. (B) Expert subjects' performance over the 5 days of training. Bold line shows the*
414 *group average, thin lines show individual subjects (each point is a mean over 3 trials with the*
415 *same searchlight length, 100%). (C) Expert subjects' performance over the 5 days of training*
416 *with the performance on the first day subtracted.*

417

418

419 Over the course of five training days, the experts' accuracy increased from $66.9 \pm 8.0\%$ to
420 $79.6 \pm 6.4\%$ (mean \pm SD across subjects, first and last training day respectively) as shown on Figs
421 1B-C, with the difference being easily noticeable and statistically significant ($p = 8 \cdot 10^{-7}$, $z = 4.9$,
422 Wilcoxon signed rank test; Cohen's $d = 1.8$, $N = 32$). As all paths generated during the training
423 were different, this difference cannot be ascribed to memorizing the path, therefore this
424 improvement represents the genuine acquisition of the skill of path tracking.

425

426 **Searchlight testing**

427 To unravel the mechanisms of skill acquisition we designed testing trials called “searchlight
428 trials”, during which subjects had to track curved paths as usual but could only see a certain
429 part of the path (fixed distance s) ahead of the cursor. The searchlight length s varied between
430 10% and 100% of the whole path length in steps of 10% (the minimal s was ~ 3 cm) to probe
431 subjects' planning horizon. Searchlight testing was conducted after 5 days of training for
432 experts or immediately for novices. During the testing block all subjects completed 30 one-
433 minute-long trials (three repetitions of each of the 10 values of s). The average accuracy at full
434 searchlight $s = 100\%$ was $82.8 \pm 7.5\%$ for the expert group and $65.7 \pm 8.4\%$ for the naïve group
435 (mean \pm SD across subjects), with the difference being highly significant ($p = 2 \cdot 10^{-9}$, $z = 6.0$,
436 Wilcoxon-Mann-Whitney ranksum test, Cohen's $d = 2.2$, $N = 62$). The performance of the naïve
437 subjects matched the initial performance of the expert subjects on their first day of training.

438

439 Before we present the rest of the data, let us consider several possible ways in which the
440 accuracy can depend on the searchlight length (Fig. 2A). For each subject, accuracy should be
441 a non-decreasing function of searchlight length. The data presented in Poulton (1974) indicate

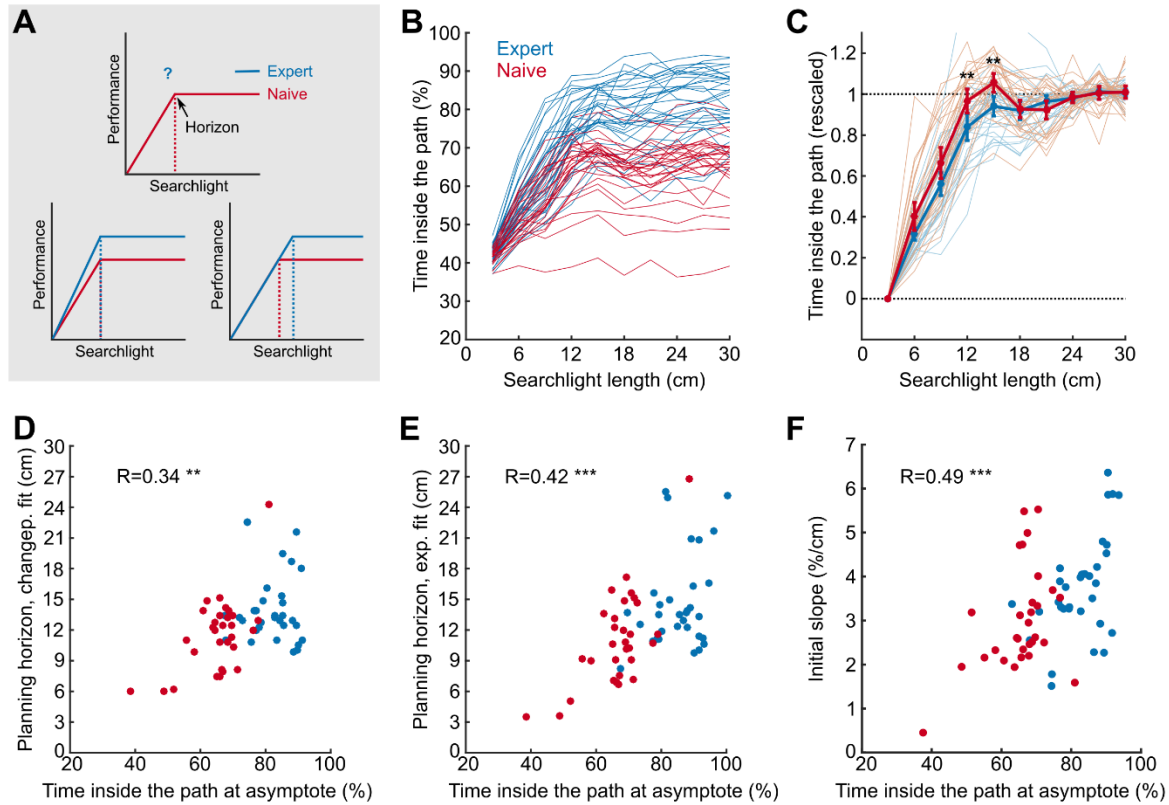
442 that this function tends to become flat, i.e. subjects reach a performance plateau, after a certain
443 value of the searchlight length that we will call *planning horizon* (Fig. 2A, top), while we
444 assume all subjects will be constrained to the similar poor performance at the smallest
445 searchlight. For the expert group, this function has to reach a higher point at $s=100\%$, but it
446 could do so because the initial rise becomes steeper, for example due to lower motor variability
447 (Fig. 2A, bottom left), or because the initial rise continues longer, i.e. planning horizon
448 increases (Fig. 2A, bottom right), or possibly both.

449

450 Fig. 2B shows subjects' accuracy in the searchlights trials as a function of the searchlight length
451 s . All subjects were strongly handicapped at short searchlights, and at the shortest searchlight
452 the performance of the two groups was similar with experts being only marginally better
453 ($42.5\pm 2.3\%$ for the expert group, $41.4\pm 1.8\%$ for the naïve group, $p=0.042$, $z=2.0$ Wilcoxon
454 ranksum test; Cohen's $d=0.5$, $N=62$).

455

456



457

458

459 *Figure 2. Searchlight testing. (A) Expert subjects were trained to have a higher performance*
 460 *at full searchlight length (top). This could be achieved by an increased initial slope (bottom*
 461 *left) at smaller searchlight length and/or an increased planning horizon as indicated with*
 462 *dashed vertical lines (bottom right). (B) Mean tracking performance for each searchlight*
 463 *length for each individual subject, in blue for the expert group and in red for the naïve group.*
 464 *Faint lines show individual subjects and bold lines show group means. (C) Mean tracking*
 465 *performance for each searchlight length, rescaled for each subject to start at 0 and end at 1*
 466 *(see text). Error bars indicate 95% confidence intervals around the means, stars indicate*
 467 *significance between the groups (**: $p < 0.01$, Wilcoxon rank sum test, Bonferroni-Holm*
 468 *corrected for multiple comparisons). (D-E) Planning horizon for each subject was defined by*
 469 *fitting a changepoint linear-constant curve (D) or an exponential curve (E) (see text). Both*
 470 *models yield an asymptote performance for each subject; the changepoint model yields a*

471 *horizon length and the exponential fit yields an “effective” horizon length. The scatter plots*
472 *show relation between the asymptote performance (as a proxy for subjects' skill) and their*
473 *planning horizon. Spearman's correlation coefficients are shown on the plot (**: $p < 0.01$, ***:*
474 *$p < 0.001$). Colour of the dot indicates the group. (F) Relationship between the asymptote*
475 *performance and the initial slope in in the changepoint linear-constant model, colours and*
476 *values as in D&E (***: $p < 0.001$).*

477

478

479 Visual inspection of Fig. 2B suggests that both effects sketched in Fig. 2A contribute to expert
480 performance. (i) the planning horizon for the expert group was longer than for the naïve group;
481 and (ii) the expert group had higher accuracies in the initial part of the performance curve,
482 before the performance plateaus, which could be explained by decreased motor variability.

483

484 To better visualize the change in performance across searchlight lengths, we linearly rescaled
485 each subject's performance curve, first by subtracting the mean performance at $s=10\%$ and then
486 by dividing by the asymptote performance (computed as the mean performance across $s=80-$
487 100%). The resulting curves all start at 0 and end at 1 (Fig. 2C). We observed a significant
488 difference between the groups at $s=40\%$ & 50% ($p=0.005$ and $p=0.004$ respectively, Wilcoxon
489 ranksum test, p -values adjusted for testing 6 searchlight lengths between 20% and 70% with
490 Holm-Bonferroni procedure, $N=62$), indicating that while naïve subjects had reached their
491 plateau by then, the expert subjects kept increasing their performance. For this analysis we
492 removed two naïve subjects with essentially flat searchlight curves (Fig. 1B), as rescaling those
493 did not lead to meaningful results.

494

495 To investigate individual differences in tracking skill, we estimated the planning horizons of
496 individual subjects (Fig. 2D). For this we fit each subject's performance (y) with a changepoint
497 linear-constant curve (see Methods), where the location of the changepoint defines the horizon
498 length. We found that the novice group had an average horizon length of 11.5 ± 3.6 cm
499 (mean \pm SD; median: 12.0 cm) and the expert group a horizon length of 14.2 ± 3.5 cm (median:
500 13.2 cm), with statistically significant difference ($p=0.007$, $z=2.7$, Wilcoxon ranksum test;
501 Cohen's $d=0.8$, $N=62$). We also found a positive correlation between the horizon length and
502 the asymptotic performance ($R=0.34$, $p=0.006$, Spearman correlation, $N=62$).

503

504 In addition to the changepoint model, we also quantified the “effective” planning horizon using
505 a single exponential to fit the individual subjects' performance data (see Methods). This
506 analysis confirmed our results (Fig. 2E). We again observed a significant difference in the
507 effective horizon length between the two groups (14.76 ± 4.6 cm vs. 11.04 ± 4.7 cm, means \pm SD
508 for both groups, medians: 13.6 cm and 10.7 cm, $p=0.002$, $z=3.0$, Wilcoxon ranksum test;
509 Cohen's $d=0.8$, $N=62$). Again, we found a positive correlation between the asymptote
510 performance and the effective horizon length ($R=0.43$, $p=0.0008$, Spearman correlation,
511 $N=62$).

512

513 Not only was planning horizon positively correlated with tracking skill (the asymptote
514 accuracy), but also the initial slope of the changepoint model (3.7 ± 1.2 %/cm vs. 3.0 ± 1.2 %/cm,
515 mean \pm SD; medians: 3.6 %/cm vs. 2.6 %/cm). Fig. 2F shows that there was a positive
516 correlation between the initial slope and asymptote accuracy ($R=0.49$, $p=6.10^{-5}$ Spearman
517 correlation, $N=62$) as well as a clear difference in the initial slope between the groups ($p=0.008$,
518 $z=2.6$, Wilcoxon ranksum test; Cohen's $d=0.6$, $N=62$).

519

520 We therefore conclude that the difference between expert and naïve performances is a
521 combination of both possibilities presented in Fig. 2A. Using the expert and naïve median
522 estimates of the intercept, the slope, and the horizon in the changepoint model, we can estimate
523 the contribution of both effects on the asymptote performance. The changepoint model
524 asymptote performance for the naïve group was 63.5%, compared to 78.7% for the expert
525 group. The model performance of the expert group at the naïve horizon was 74.2%. Hence,
526 approximately 71% of the expert performance gain of 15.2%, was due to the increase in the
527 initial slope (possibly due to lower motor variability), and the remaining 29% can be attributed
528 to the increase in planning horizon. The identical procedure with mean model parameter
529 estimates instead of median estimates, yields 44% attributable to motor acuity and 56%
530 attributable to planning horizon. We conclude that between a third and a half of the expert
531 performance gain is attributable to their increase in planning horizon.

532

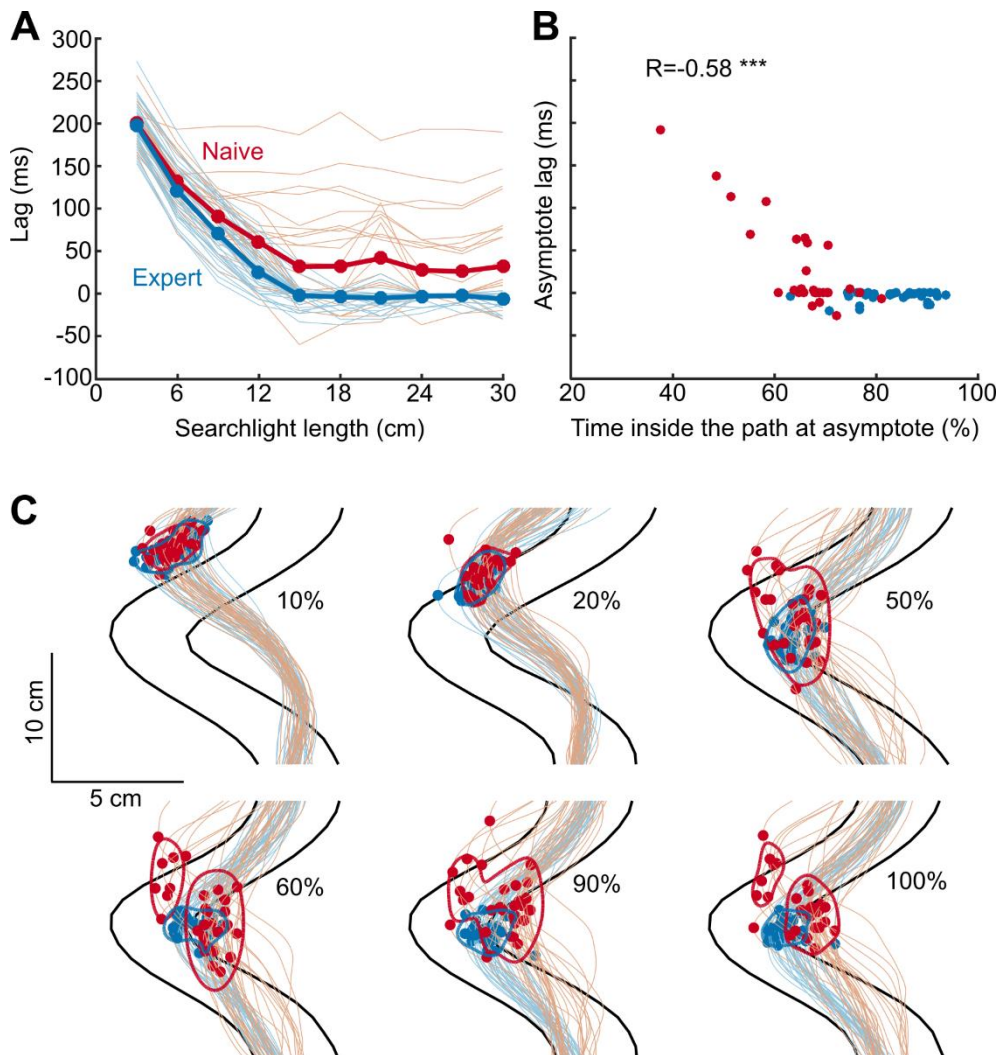
533 **Trajectory analysis**

534 Naïve subjects performed worse than the expert subjects at long searchlights but all subjects
535 performed almost equally badly at short searchlights. What kinematic features can these
536 differences be attributed to?

537

538 Clearly, at short searchlights, performance has to be reactive. To measure how quickly changes
539 in the path were reflected in the motor commands, we computed the time lag between cursor
540 trajectory and path midline (the lag maximizing cross-correlation between them). As Fig. 3A
541 shows the lag was ~200 ms at $s=10\%$ for all subjects and dropped to ~0 ms at $s=50\%$ for the
542 expert group. While many naïve subjects also decreased their lags to zero, 10 out of 30 never
543 achieved the 0 ms lag. The five naïve subjects showing the largest lags at large searchlights

544 were also those with the worst performance (Fig. 3B). Therefore, there was a strong negative
545 correlation between the asymptote lag (mean across $s=80-100\%$) and the asymptote
546 performance (mean across $s=80-100\%$) of $R=-0.58$ (Fig. 3B, $p=8 \cdot 10^{-7}$, Spearman correlation,
547 $N=62$).
548



549
550

551 *Figure 3. Analysis of trajectories. (A) Mean time lag between cursor trajectory and path*
552 *midline, for each searchlight length for each individual subject (faint lines) and mean of per-*
553 *subject values (bold lines), in blue for the expert group and in red for the naïve group. (B)*
554 *Asymptote lag and asymptote performance across subjects. Correlation coefficient is shown on*

555 *the plot (** $p < 0.001$). Colour of the dot indicates the group. (C) Average per-subject*
556 *trajectories in sharp bends (leftward bends were flipped to align them with the rightward*
557 *bends). Each trajectory is averaged across approximately 40 bends (the number of bends*
558 *varied across searchlight lengths). Colour of the lines indicates the group. Black lines show*
559 *average path contour. Dots show turning points of the trajectory. Contour lines show the kernel*
560 *density estimate 75% coverage areas. Subplots correspond to searchlight lengths $s=10\%$, 20% ,*
561 *50% , 60% , 90% and 100% .*

562

563 Next, for each testing path we found all segments exhibiting sharp leftward or rightward bends
564 (see materials and methods, our inclusion criteria yielded 13 ± 5 segments per path, mean \pm SD).
565 For each searchlight length s and for each subject, we computed the average cursor trajectory
566 over all segments ($N=38 \pm 8$ segments per searchlight) after aligning all segments on the bend
567 position (Fig. 3C, leftward bends were flipped to align them with the rightward bends). At
568 $s=10\%$ all subjects from both groups follow very similar lagged trajectories, resulting in low
569 accuracy. As searchlight increases, expert subjects reach zero lag and choose more and more
570 similar trajectories, whereas naïve subjects demonstrate a wide variety of trajectories with some
571 of them failing to reach zero lag and others failing to keep the average trajectory inside the path
572 boundaries. To visualize this, we plotted the kernel density estimate 75% coverage contour of
573 inflection points for each group. As the searchlight increases, the groups become less
574 overlapping and the naïve group appears to form a bimodal distribution (Fig. 3C).

575

576 In summary, at very short searchlights all subjects performed poorly because in this reactive
577 regime their trajectories lagged behind the path. At longer searchlights the expert subjects were
578 able to plan their movement to accommodate the bends (the longer the searchlight the better),

579 but naïve subjects failed to do so in various respects: either still lagging behind or not being
580 able to plan a good trajectory.

581

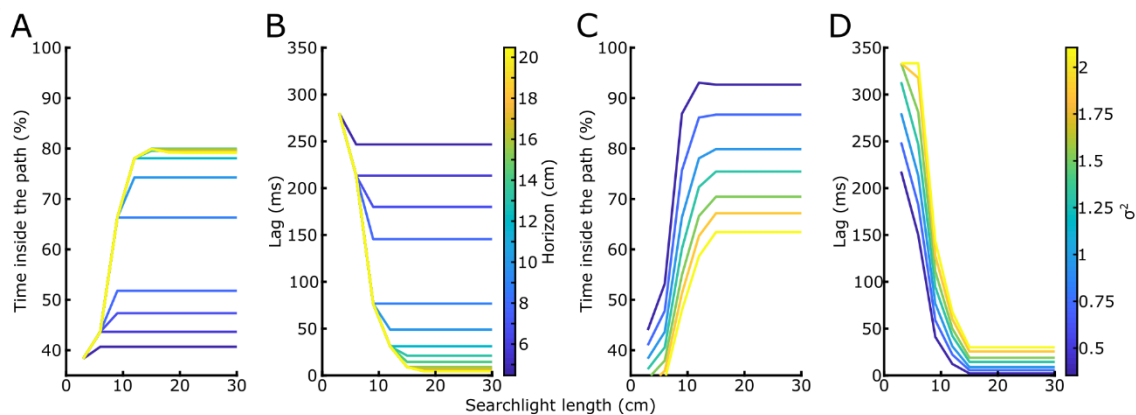
582 **Receding horizon model analysis**

583 Next, we modelled subjects' behaviour by receding horizon control (RHC) to illustrate that
584 such an approach is able to capture some crucial features of the behavioural data. In RHC a
585 sequence of motor commands is computed to minimize the expected cost over a future time
586 interval of finite length, i.e. the horizon. After the first motor command is applied, the
587 optimization procedure is repeated using a time interval shifted one time step ahead. See
588 Methods section for a more detailed and formal description of RHC. As cost function, we used
589 the weighted sum of a measure of inaccuracy (i.e. probability of being outside the path) and
590 the magnitude of the motor cost (see Methods for details). Cost function with a similar trade-
591 off between movement accuracy and motor command magnitude have been used previously to
592 describe human motor behaviour in different tasks (Braun et al. 2009; Diedrichsen 2007;
593 Todorov and Jordan 2002). The model has four different parameters: horizon (h), motor noise
594 (σ^2), motor delay (τ) and motor command penalty weight (λ).

595 We ran the model on the experimental paths to obtain simulated movement trajectories from
596 which task performance and lag could be computed in the same way as for the experimental
597 trajectories (Fig. 2 and 3). Our simulations revealed that both, a larger model horizon as well
598 as a smaller motor noise parameter increased the task performance and decreased the lag (Fig.
599 4). Hence, the experimentally observed higher performance and smaller lag of expert subjects
600 compared to naïve (Fig. 2B and 3A) could be explained either by an increased model horizon
601 or by reduced motor noise in the model. However, the searchlight length at which the task
602 performance of the model reached a plateau increased with model horizon and did not change
603 or even decreased with a smaller motor noise parameter (Fig. 4A, C). Experimentally, on the

604 other hand, we observed that subjects with a higher task performance reached their
605 performance plateau at higher searchlights (Fig. 2D, E). This correlation between performance
606 and plateau onset, that was observed experimentally, cannot be explained by the variation of
607 the motor noise parameter across subjects, but is only consistent with an increase of the model
608 planning horizon for subjects with higher performance.

609



610

611 *Figure 4: Task performance and lag as a function of searchlight length for model simulations*
612 *with different horizons (A,B) or different amounts of motor noise (C,D). A motor noise of $\sigma^2=1$*
613 *was used for (A,B) and a horizon of $h=15\text{cm}$ for (C,D). The motor delay and motor command*
614 *penalty weight were fixed at $\tau=200\text{ms}$ and $\lambda=0.5$ in all simulations.*

615

616 Next, we used Bayesian inference to estimate the model parameters from the experimentally
617 observed movement trajectories (see Methods for details). Based on inferred distributions of
618 parameter values, we then predicted task performance and lag for each subject. To avoid over-
619 fitting cross-validation was used, i.e. fitting and prediction was done on different trials. Model
620 task performance and lag resembled the experimentally observed task performance and lag
621 with regard to their change across searchlights as well as with regard to the difference between
622 naïve and the expert subjects (Fig. 5A,B). On a single subject and trial level there was a high

623 correlation between model and experimental task performance (Fig. 5C, Spearman correlation
624 $r=0.9$, $R^2=0.84$) and lags (Fig. 5D, Spearman correlation $r=0.87$, $R^2=0.88$).

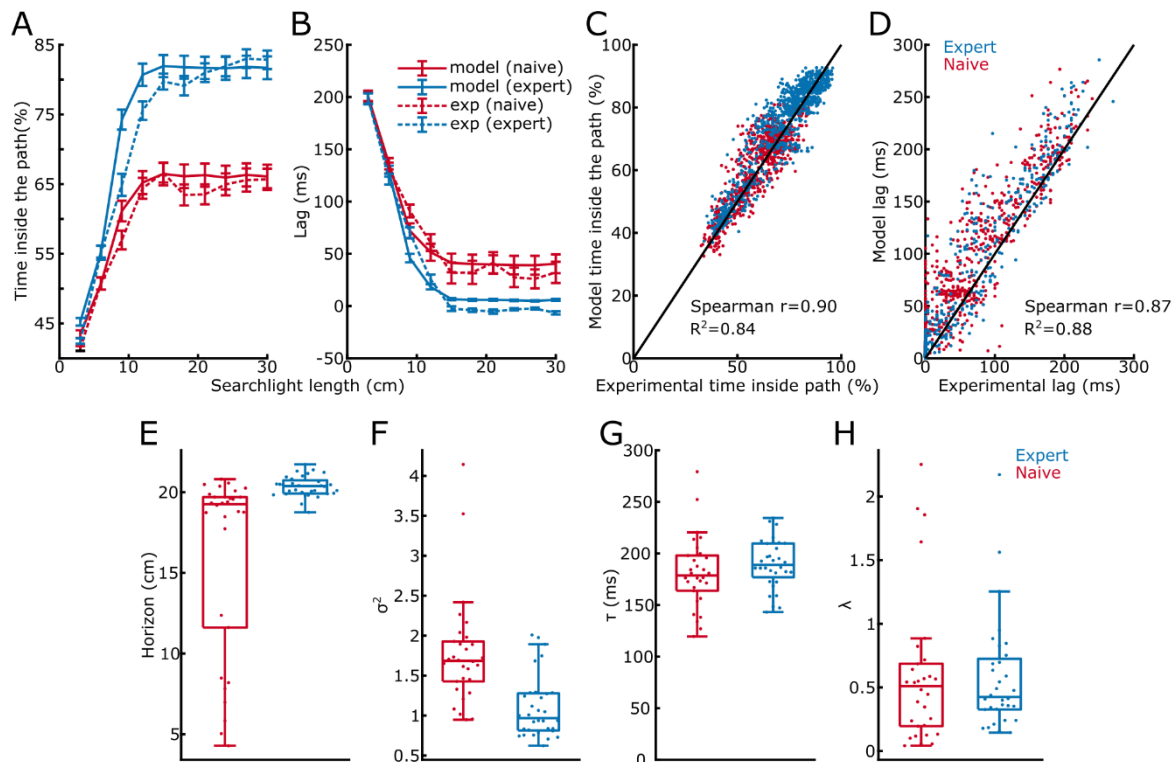
625

626 We compared the estimated model parameters between expert and naïve subjects. The fitted
627 model horizon was higher for the expert group than for the naïve group (Fig. 5E, Wilcoxon
628 ranksum test: $z=4.84$, $p=1\cdot 10^{-6}$, $N=62$) and was correlated with the horizon obtained from the
629 change point analysis (Spearman correlation, $r=0.48$, $p=7\cdot 10^{-5}$, $N=62$) and the exponential fits
630 (Spearman correlation, $r=0.43$, $p=6\cdot 10^{-4}$, $N=62$). One caveat here is that there was large
631 uncertainty in the estimates of model horizon for most subjects, and the exact values shown in
632 Fig. 5E might be systematically biased due to some model misspecification (in particular, note
633 that the values in Fig. 5E are all larger than the estimates in Fig. 2D,E). That said, the RHC
634 model estimates qualitatively agree with our earlier estimates that the expert horizons were
635 larger than the naïve horizons.

636

637 The fitted motor noise was significantly lower for the expert than for the naïve group (Fig. 5F;
638 Wilcoxon ranksum test: $z=4.66$, $p=3\cdot 10^{-6}$, $N=62$) while the delay and the penalty parameters
639 were not different (Fig. 5G,H; delay: Wilcoxon rank sum test, $z=1.50$, $p=0.13$; penalty:
640 Wilcoxon rank sum test, $z=0.528$, $p=0.60$, $N=62$). In the model, lower motor noise lead to
641 steeper initial accuracy slope (Fig. 4C). The expert group having lower estimated motor noise
642 hence agrees well with our observation that experts had steeper initial accuracy slope (Fig. 2F).

643



644

645 *Figure 5: Comparison between the receding horizon model and subjects' behaviour. A,B: Task*
 646 *performance and lag as a function of the searchlight for expert and naive subjects for the*
 647 *experiments and model simulations. C,D: Scatter plot of model and experimental task*
 648 *performance and lag for each trial of each subject. E-H: Model parameters for the subjects*
 649 *from the naive and the expert group. Each dot depicts one subject, boxplots show medians as*
 650 *well as first and third quartiles.*

651

652 Using the model fits obtained above, we estimated how much of the experts' gain in asymptote
 653 performance was due to increased horizon vs. decreased noise. To do this, we simulate the
 654 model with naive group parameters but expert group horizons (see Methods). This brings the
 655 performance almost half-way to the expert performance (for large searchlights the performance
 656 levelled off at 72% instead of 82% with lower horizon, compared to 66% for the naive
 657 subjects). We observe roughly the same increase (to 75%) when we simulate the model with
 658 naive group parameters but expert group noise levels. Similarly, when we use expert group

659 parameters but naïve group horizons or noise levels, the performance drops approximately half-
660 way to the naïve accuracy (74% for naïve horizon, 71% for naïve motor noise). In contrast, the
661 delay and the motor penalty parameters had less influence on the asymptote performance (63%
662 and 64% for naïve group parameters with expert delay or motor penalty; 80% for expert group
663 parameters with naïve delay or motor penalty). From this we conclude that the increase in the
664 experts' performance was caused by equal measures through an increase in planning horizon
665 and the decrease in motor noise. This is in a good qualitative agreement with the conclusions
666 we presented earlier based on the linear changepoint fits.

667

668 **Discussion**

669

670 We used a paradigm that allowed us to study skill development when humans had to track an
671 unpredictable spatial path. The skill requires fast reactions to new upcoming bends in the road,
672 but also a substantial “planning ahead” component – i.e. the anticipation and preplanning of
673 movements that have to be made in the near future. We used the accuracy, i.e. the fraction of
674 time the cursor was inside the path boundaries, as the measure of performance. We observed a
675 substantial improvement in accuracy after 5 days of training (Fig. 1B,C). The paths were
676 different on every trial, so the improvement in performance cannot be attributed to a memory
677 for the sequence.

678

679 What changes in the motor system occur through learning that allowed skilled subjects to
680 perform better? One component of this improvement has been previously called “motor acuity”
681 (Shmuelof et al. 2012, 2014) and corresponds to the subjects’ ability to execute motor
682 commands more accurately, i.e. due to the lower motor variability. We hypothesized that an
683 additional component is an increased ability to take into account approaching path bends and
684 to prepare for an upcoming movement segment. We directly estimated both effects by using a
685 searchlight testing where only a part of the approaching curve was visible. In agreement with
686 our hypothesis, we found that subjects with a higher tracking skill demonstrated larger planning
687 horizons: on average ~14cm for the expert group vs. ~11cm for the naïve group, corresponding
688 to the time horizons of ~0.4s and ~0.3s respectively. Our results suggest that the increase in
689 planning horizon is not an epiphenomenon but is causally related to the performance increase,
690 as expert subjects showed worse performance when the searchlight was reduced below their
691 planning horizon (Figure 2C). We estimated that in our experiments between a third and a half
692 of the increased performance after practice can be attributed to an increased planning horizon

693 while the rest can be accounted for by a reduction in the motor variability which may be
694 interpreted as higher motor acuity.

695

696 The expert group showed higher initial slope of the searchlight-accuracy curve. We interpreted
697 this as an indirect evidence for lower motor variability, even though other explanations for
698 higher slope are in principle also possible. Our assumption was that as long as the searchlight
699 lengths does not exceed a subject's horizon, all subjects (expert and naive) are able to use
700 information about the whole visible path chunk. The results of the RHC fits showed a clear
701 difference in motor noise between the groups, in agreement with our interpretation that the
702 expert group had lower motor variability.

703

704 Note that “planning”/“preparing” the movement can be interpreted differently depending on
705 the computational approach. In the framework of optimal control (Todorov and Jordan 2002),
706 subjects do not plan the actual trajectory to be followed, but instead use an optimal time-
707 dependent feedback policy and then execute the movement according to this policy. The
708 observed increase in planning horizon can be interpreted in the framework of model predictive
709 control, also known as receding horizon control, RHC (Kwon and Han 2005). In RHC, the
710 optimal control policy is computed for a finite and limited planning horizon, which may not
711 capture the whole duration of the trial. This policy is then applied for the next control step,
712 which is typically very short, and the planning horizon is then shifted one step forward to
713 compute a new policy. Hence, RHC does not use a pre-computed policy, optimal for an infinite
714 horizon, but a policy which is only optimal for the current planning horizon. Increasing the
715 length of the planning horizon is therefore likely to increase the accuracy of the control policy.
716 In our experiments this would allow for a larger fraction of time spent within the path
717 boundaries. We designed a simple RHC model to test directly which components in the model

718 would have to change through training to quantitatively explain the subject's behaviour. The
719 dynamics of movement and the cost function were modelled in line with previous studies that
720 used optimal control to describe human behaviour in various motor control and learning tasks
721 (Braun et al. 2009; Diedrichsen 2007; Todorov and Jordan 2002). We fitted the RHC model to
722 the behaviour of each subject and found that it was able to fit the data very accurately (Fig. 5).
723 The experimentally observed differences between expert and naïve subjects were reflected in
724 the model fits by higher planning horizons and lower motor noise parameters in the expert
725 group. Our findings, thus, demonstrate that subjects' behaviour can be understood in the
726 context of RHC, and longer planning horizons of the expert group indicate that subjects learn
727 how to take advantage of future path information to improve motor performance.

728

729

730 Despite a clear difference in the distribution of planning horizons between the naive and the
731 expert groups (Fig. 2D), there was a substantial overlap: the planning horizon of many naive
732 and expert subjects were similar. While this might simply reflect a moderate effect size
733 combined with inter-subject variability and measurement noise, it also remains a possibility
734 that the difference between groups was largely caused by those naive subjects with very low
735 horizons and expert subjects with very high horizons.

736

737 **Related work**

738 Ideas like the RHC were put forward in a recent study (Ramkumar et al. 2016) that suggested
739 that movements are broken up in 'chunks' in order to deal with the computational complexity
740 of planning over long horizons. That study suggests that monkeys increase the length of their
741 movement chunks during extended motor learning over the course of many days which may
742 be explained by monkeys increasing their planning horizon with learning. At the same time,

743 the efficiency of movement control within the chunks improved with learning which may also
744 be the result of a longer horizon. Despite these potential consistencies with our approach we
745 note that in their model Ramkumar et al. (2016) assumed that ‘chunks’ are separated by halting
746 points (i.e. points of zero speed) and movements within ‘chunks’ are optimized independently
747 from each other. Our RHC model does not have independent movement elements but
748 movements are optimized continuously.

749

750 Even though our study, to the best of our knowledge, is the first to directly investigate the
751 evolution of the planning horizon during continuous path tracking, an increase in the planning
752 horizon after learning has been recently demonstrated when learning sequences of finger
753 movements (Ariani et al. 2020). Similar path tracking tasks have been used before (Poulton
754 1974). Using a track that was drawn on a rotating paper roll, these early studies found that the
755 accuracy of the tracking increased with practice and with increasing searchlight length (which
756 was modified by physically occluding part of the paper roll, (Poulton 1974), p 187). These
757 studies, however, did not investigate the effect of learning on the planning horizon.

758

759 More recent studies used path tracking tasks where the goal was to move as fast as possible
760 while maintaining the accuracy (instead of moving at a fixed speed). In all of these studies the
761 identical path was repeatedly presented. In one study subjects had to track a fixed maze without
762 visual feedback and learnt to do it faster as the experiment progressed (Petersen et al. 1998);
763 there the subjects had to once “discover” and then remember the correct way through the maze.
764 In another series of experiments, Shmuelof et al. asked subjects to track two fixed semi-circular
765 paths. Subjects became faster and more accurate over the course of several days (Shmuelof et
766 al. 2012), but this increase in the speed and accuracy did not generalize to untrained paths
767 (Shmuelof et al. 2014). In contrast to these previous path tracking studies, we used randomly

768 generated paths throughout the experiment. By investigating the generalization of the path
769 tracking skill to novel paths we could reveal an increasing planning horizon with learning.

770

771 **Conclusion**

772 In conclusion, we have established that people are able to learn the skill of path tracking and
773 improve their skill over 5 days of training. This increase in motor skill is associated with the
774 increased motor acuity and increased planning horizon. The dynamics of preplanning can be
775 well described by a receding horizon control model.

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784 **Author Contribution**

785 Conceptualization, LB. DK. and CM; Methodology, LB. DK. JD and CM; Formal Analysis,
786 LB. DK and CM; Writing – Original Draft, LB. DK and CM; Writing – Review and Editing,
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