

The effects of probabilistic context inference on motor adaptation

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8 Humans have been shown to adapt their movements when sudden or gradual changes to
9 the dynamics of the environment are introduced, a phenomenon called motor adaptation.
10 If the change is reverted, the adaptation is also quickly reverted. Humans are also able
11 to adapt to multiple changes in dynamics presented separately, and to be able to switch
12 between adapted movements on the fly. Such switching relies on contextual information
13 which is often noisy or misleading, which affects the switch between adaptations. Recently,
14 the COIN computational model for motor adaptation and context inference was introduced,
15 which contains components for context inference and Bayesian motor adaptation. This
16 model was used to show the effects of context inference on learning rates across different
17 experiments. We expanded on that work by using the COIN model to show that the effects
18 of context inference on motor adaptation and control go even further than previously shown.
19 Here, we used the COIN model to simulate classical motor adaptation experiments from
20 previous works and showed that context inference, and how it is affected by the presence
21 and reliability of feedback, effect a host of behavioral phenomena that had so far required
22 multiple hypothesized mechanisms, lacking a unified explanation. Concretely, we show that
23 the reliability of direct contextual information, as well as noisy sensory feedback, typical
24 of many experiments, effect measurable changes in switching-task behavior, as well as in
25 action selection, that stem directly from probabilistic context inference.

Introduction

It has been shown that humans can adapt motor commands to counteract changes in the dynamics of the environment and their own bodies, such as performing reaching movements with a weight attached to the wrist. This is known as motor adaptation. Moreover, human participants have been shown to adapt to different, even opposing, changes during the course of a single experiment (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Shadmehr & Brashers-Krug, 1997). Additionally, humans have been shown to dynamically switch between different

33 learned adaptations (Davidson & Wolpert, 2004; Ethier, Zee, & Shadmehr, 2008; Lee &
34 Schweighofer, 2009).

35 By introducing blocks of trials in which body dynamics are altered (e.g. a mechanical
36 arm exerts a force on the participant's hand), experimenters are able to observe motor
37 adaptation through the lens of motor error. Across many different motor adaptation exper-
38 iments (e.g. Davidson & Wolpert, 2004; Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi,
39 1994), well-established phenomena have been observed: (i) the ability to recall previously-
40 learned skills, called savings; (ii) the ability to return to unmodified dynamics, termed
41 de-adaptation; (iii) the interference in motor learning between opposing manipulations in
42 dynamics, called anterograde interference; (iv) spontaneous display of behavior consistent
43 with a previously-learned adaptation, during trials where errors are forced to be zero, called
44 spontaneous recovery.

45 To explain these phenomena, a number of computational models have been introduced,
46 which adapt their motor commands after observing motor errors. The most studied are
47 linear learners (Forano & Franklin, 2020; Scheidt, Dingwell, & Mussa-Ivaldi, 2001; Smith,
48 Ghazizadeh, & Shadmehr, 2006), but Bayesian accounts have also been presented, providing
49 an alternative explanation for savings and quick de-adaptation in the form of switching
50 between forward models (Kording & Wolpert, 2004; Oh & Schweighofer, 2019).

51 While these general models of adaptation explain the most common phenomena observed
52 in experiments, other known phenomena remain outside of their scope. For example, it is
53 known that adaptation rate is reduced in situations where the environment is unstable and
54 unpredictable (Herzfeld, Vaswani, Marko, & Shadmehr, 2014), or situations in which errors
55 are small (Marko, Haith, Harran, & Shadmehr, 2012) or adaptations slowly introduced
56 (Huang & Shadmehr, 2009). Action selection has also been found to depend on the history
57 of adaptations learned (Davidson & Wolpert, 2004; Vaswani & Shadmehr, 2013).

58 Recently, a new computational model for context-dependant motor learning based on
59 Bayesian inference was introduced by Heald, Lengyel, and Wolpert (2021), called COIN
60 (for context inference). Heald et al. (2021) formalized context inference as a process that
61 operates independently from motor learning, but is informed by it, establishing a loop
62 whereby context inference also informs motor learning. With this model, Heald et al. (2021)
63 showed that context inference causes the observed changes in the rate of motor learning in
64 previous experiments (e.g. Herzfeld, Kojima, Soetedjo, & Shadmehr, 2018).

65 In this work, we use the COIN model to show that the process of context inference
66 underlies more behavioral phenomena than previously shown. We focused on the effects of
67 uncertain contextual information on switching behavior, especially during so-called error-
68 clamp trials, in which errors are forced to zero by experimenters. More specifically, we
69 focused on the effects of perceptual noise, as well as feedback modalities, in context infer-
70 ence, which in turn affects behavior in ways that can be directly measured. We show that
71 through context inference, switching behavior can display three main effects that have been
72 previously attributed to hypothesized ad-hoc mechanisms: (1) The size of an adaptation
73 dictates how quick and reliable switching between tasks is Kim, Ogawa, Lv, Schweighofer,

74 and Imamizu (2015); Oh and Schweighofer (2019), which we explain in terms of the effects
75 of perceptual noise on context inference. (2) Previously-learned adaptations can interfere
76 with switching behavior (Davidson & Wolpert, 2004), which we explain in terms of uncertain
77 context inference. (3) Training history (i.e. which adaptations have been learned and for
78 how long) affects switching during error-clamp trials (Vaswani & Shadmehr, 2013), which
79 we also attribute to uncertain context inference. To do this, we used the COIN model to
80 simulate the experimental setups and the decision-making agents (i.e. participants) during
81 those experiments.

82 With these combined simulations and their qualitative comparison to the experimental
83 phenomena outlined, we provide further evidence that context inference may be a single
84 coherent and mechanistic account that underlies experimentally well-established motor
85 adaption and history effects under changing contexts.

86

Results

87 Using the COIN model (Heald et al., 2021), we simulated representative experiments
88 from a number of experimental studies on motor adaptation to illustrate how this model
89 explains different experimental findings using the dynamics of context inference. We will
90 present these simulations alongside the experimental results from the representative studies
91 and discuss in detail how context inference explains the experimental phenomena.

92 Before presenting these results, we briefly describe the COIN model, leaving a more
93 thorough explanation for the methods section. Additionally, we present simulations using
94 the model that show the effects of contextual cues and perceptual noise on context inference,
95 which pave the way for the simulated experiments that we show later on.

96 **Modeling context-dependent adaptation**

97 We focused on three main components of the COIN model: (1) context inference, (2)
98 motor adaptation and (3) action selection. The processes defined by these component occur
99 in this order, and each component informs the ones that follow.

100 Central to the model is the concept of context, defined in terms of the task to be per-
101 formed, the variables of the environment that are relevant to perform the task, the forward
102 models used by the decision-making agent to perform the task, and the update mechanisms
103 necessary to adapt these forward models to the changing environment. Together, these
104 elements allow the agent to make predictions on future observations when this context is
105 active, and these predictions are used to infer the context. For example, when lifting an
106 object of unknown weight, an agent might have learned one context for heavy objects and
107 one for light objects. When observing an object to be lifted, the agent can use its size and
108 texture to estimate the weight of the object, which in turn allows the agent to infer the
109 appropriate context and, with it, decide how to lift the object.

The COIN model contains, additionally to these three main components, components for learning new contexts (i.e. inferring the existence of a new context that had not been previously encountered by the agent), as well as the ability to infer subject-specific parameters such as a participant's assumed transition probabilities between contexts, which can differ from the real, hidden transition probabilities. In this work, we focused on switching behavior between previously-learned contexts, as well as in the perceptual aspect of context inference. More specifically, we simulated previous experiments and focused on the way the COIN model qualitatively explains experimental phenomena observed in these experiments. To do this, we fixed both the transition probabilities between contexts and the number of contexts based on the real values during the experiments, which were made available to participants. Fixing these values, in turn, allowed us to simplify the generative model, internal to the agent, using conjugate priors, with which the agent can do exact Bayesian inference. The generative model we used here can be seen in Figure 1A, including the priors for both context inference and motor adaptation. For more details on these choices, see the Methods section.

Contextual cues and feedback

The behavioral phenomena which are the focus of this work can be explained as arising from the effects of contextual cues and sensory feedback provided to participants during the experiment. To illustrate these effects in a simple example, we first simulated a generic motor adaptation experiment similar to those performed by Davidson and Wolpert (2004), in which participants must adapt to a visuomotor rotation of the cursor on a screen in relation to the movement of a pointing device.

The key to an intuitive understanding of the results presented below, is to observe what happens when the presence and reliability of contextual cues is varied, as well as the perceptual noise added to the cursor. In Figure 1B, a 3x3 grid of results can be seen, where each simulation in this grid is a combination of low, medium or high contextual cue reliability (where low reliability is equivalent to presenting no cues), and low, medium or high perceptual noise.

The first column of Figure 1 shows that, in the presence of reliable contextual cues, context inference is accurate, certain and fast to switch. However, as contextual cues become less reliable, switching between known contexts becomes slower, as seen in the posterior probabilities over contexts at and after trial 20 in the second and third columns. Furthermore, as perceptual noise increases, switching becomes not only slower, but also more uncertain, with individual agents incorrectly missing the switch entirely.

Additionally, the motor responses (shown in purple) can be seen to depend not only on the current estimate of the rotation angle (shown as the green line), but also the uncertainty over the current context. This is most evident in the high cue uncertainty and observation noise panel, in which the response varies substantially from the estimate of the angle (i.e. the purple line deviates from the green line), even when the real context has the highest estimated probability.

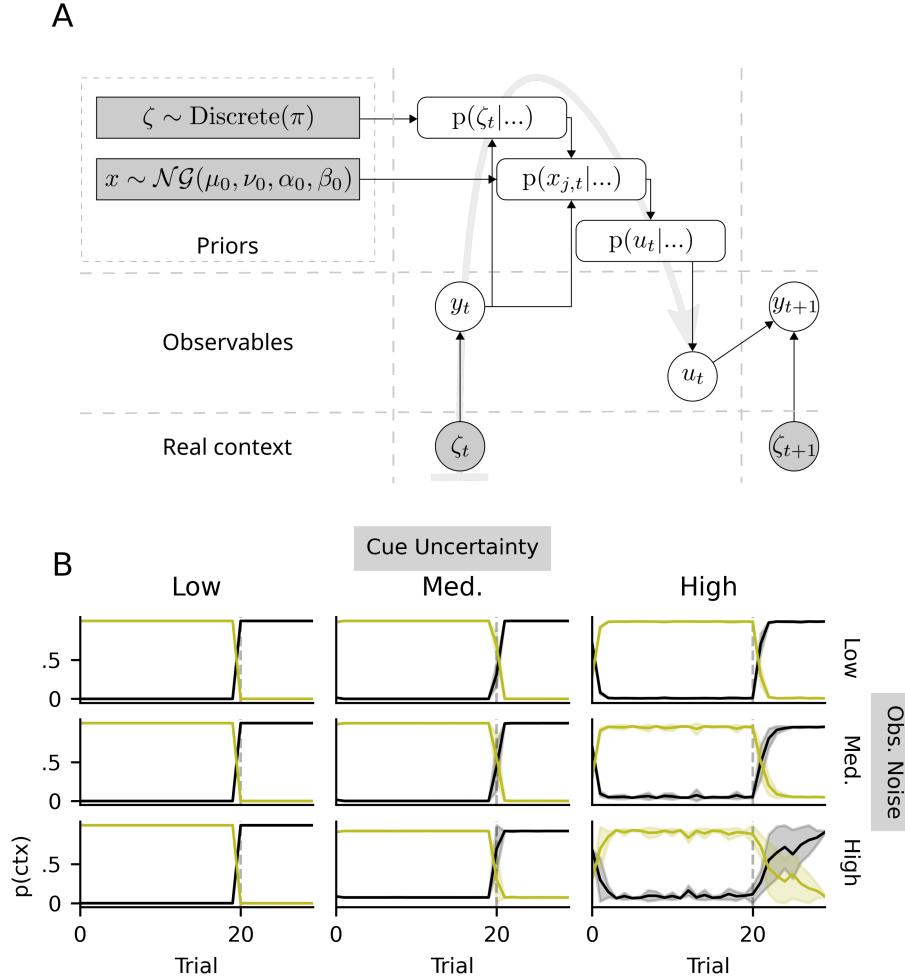


Figure 1. Schematic representation of the model and illustrative simulations. (A) Generative model. Clear circles represent the observables, i.e. motor commands u_t and direct observations y_t (e.g. cursor position). The true context ζ_t is not directly observable, but influences y_t . The dark rectangles represent the prior distributions for the inferred adaptation level x_t (Normal-Gamma distribution) and the current context ζ_t (discrete distribution with known π ; see Methods). At every trial, the context is inferred, then motor adaptation is carried out and finally a motor command is issued; the flow of this process is indicated by the gray arrow in the background, while black arrows show the direction of information flow. (B) Simulations obtained with the model in (A), using a simulated experimental setup similar to that by Davidson and Wolpert (2004), in which the context changes at trial 20 (vertical, dashed lines). A total of 3x3 experiments were simulated, with low, medium and high levels of both cue uncertainty and observation noise. Each plot represents context inference $p(\zeta_t|...)$ for one specific level of cue uncertainty and observation noise. The y-axis represents the posterior probability of each context $p(\zeta_t = j)$; the black line represents the baseline context (i.e. no adaptation), the green line represents the only adaptation to be learned during the simulated experiment. The shaded areas represent the standard deviation around the mean, obtained across 50 simulated participants.

150 As we show below, these effects are at the heart of the behavioral phenomena observed in
151 the experiments by Kim et al. (2015), Oh and Schweighofer (2019), Davidson and Wolpert
152 (2004), and Vaswani and Shadmehr (2013), which we directly simulate in this work, along-
153 side others that we discuss in the Discussion section.

154 **Experimental results**

155 In this section, we present experimentally-observed phenomena in three sections, and
156 show that the dynamics of context inference provide a unifying explanation for all of them.
157 In the first section, we discuss switches between contexts, and how slow context inference
158 affects these switches. In the second section, we focus on interference between learned
159 adaptations. Finally, in the third section we discuss context inference during error-clamp
160 trials, and its effect on behavior. For each of the three sections, we selected one or two
161 studies which are representative of the phenomenon being discussed.

162 For clarity, we first introduce necessary terminology that is typically used in experimen-
163 tal studies. As an example, we will use a typical motor adaptation task in which participants
164 have to make reaching movements while holding the handle of a mechanical arm that exerts
165 a curl force on the participant’s hand. Depending on the trial, the mechanical arm might
166 exert a curl force in a clockwise or counter-clockwise direction, or no force at all. Let us
167 define the baseline context O as that in which the mechanical arm exerts no force. Contexts
168 A and B can be defined as those with clockwise or counter-clockwise, respectively. Abusing
169 notation, a usual statement is that $B = (-A)$, as the forces have the same magnitude but
170 point in opposite directions. Similarly, one can define context A/2, with the same direction
171 of adaptation as A, but half the magnitude. Finally, many experiments include a block of
172 error-clamp trials at the end of the experiment, in which the mechanical arm forces the
173 participant to make straight-line movements; we represent these with the letter E.

174 With this terminology, a typical experiment (e.g. Ethier et al., 2008) would have a block
175 structure of O-A-B-E, or O-A-(-A)-E, which means that the participant goes through a
176 block of trials with no external force applied (O), a number of trials with a clockwise curl
177 force (A), a block with counter-clockwise forces (B), and finally a block with error-clamp
178 trials (E). With repeated contexts (e.g. Oh & Schweighofer, 2019), an experiment can be
179 described as $O_1-A_1-O_2-\dots$.

180 **Savings and slow/fast switching.** The term ‘savings’ refer to the ability to remem-
181 ber a previously-learned adaptation and apply it without having to re-learn it. Savings is
182 almost universally observed in humans (Brashers-Krug, Shadmehr, & Bizzi, 1996; Medina,
183 Garcia, & Mauk, 2001; Shadmehr & Brashers-Krug, 1997; Smith et al., 2006; Zarahn, We-
184 ston, Liang, Mazzoni, & Krakauer, 2008). In an O-A-O-A experiment, for example, savings
185 would express themselves in the second A block in the form of a much higher adaptation rate
186 than that observed during the first A block. The related concept of quick de-adaptation
187 occurs in A-O transitions, where participants switch back to baseline without having to
188 re-learn it.

189 In this section, we discuss savings and de-adaptation in terms of switching between
190 contexts. We show that through context inference and how it is affected by contextual cues
191 and observation noise, savings are not immediate, but a relatively fast process that reflects
192 context inference.

193 To show this, we examined multiple experimental studies in which savings are observed.
194 We categorized these studies based on the amount of contextual information made available
195 to participants: In some experiments (e.g. Kim et al., 2015; Lee & Schweighofer, 2009), the
196 context is clearly revealed to the participant using sensory cues. We call these cued-context
197 experiments. In other experiments, partial information is available to participants (e.g.
198 Davidson & Wolpert, 2004; Zarahn et al., 2008) in the form of large prediction errors,
199 partial contextual information or reward prediction errors; we refer to these as partially-
200 cued experiments.

201 We selected three representative experiments from two studies (Kim et al., 2015; Oh &
202 Schweighofer, 2019) which differ in the amount of contextual information available to par-
203 ticipants. Kim et al. (2015) performed a cued-context visuomotor rotation experiment with
204 three contexts with different rotation: no rotation, 40 degrees and -40 degrees. Participants
205 performed shooting movements in blocks of trials with the same rotation. Importantly, a
206 colored light identified the current context, making this a cued-context experiment. Con-
207 sistent with the context-inference account, the authors found that switching was immediate
208 and accurate.

209 In Figure 2A we show the results of simulations with the model using the parameters
210 of the task, as well as the experimental results from Kim et al. (2015). The correspondence
211 between simulations and experimental results can be seen in the switches between contexts
212 in the center panel, i.e. when the solid gray line (representing the true context) switches
213 between 40, 0 and -40; in both panels (second and third), the thick black line, representing
214 the agent’s adaptation, quickly follows these switches.

215 Critically, in Figure 2A it can be seen for the first four context switches (until about
216 trial 250) that participants had not yet completely adapted to the rotation, as evidenced
217 by their responses not being on par with the true rotation angle. This undershooting of
218 responses (i.e. not doing the 40 degree rotation) happens despite participants being able to
219 immediately and with high certainty identify the true context, as shown in the first-column
220 panel. These results are similar to those shown by Imamizu et al. (2007), where sensory
221 cues of varying reliability effected immediate or slow contextual switches.

222 To expand on these results, we now turn to feedback and its effects on switching behavior.
223 Oh and Schweighofer (2019) performed two partially-cued experiments with a visual rotation
224 of 20 and 10 degrees, respectively. The results of their experiments can be seen in Figure 2B
225 and 2C, alongside simulations with the COIN model. Participants in the first experiment
226 (Figure 2B) first learned the adaptation in A. In subsequent A – O transitions, participants
227 showed immediate switching (with a one-trial lag) between A and O (both ways), which
228 can be seen in their responses (black line in the last two columns of Figure 2B) closely
229 following the switches in the black line (true rotation). In the second experiment (Figure

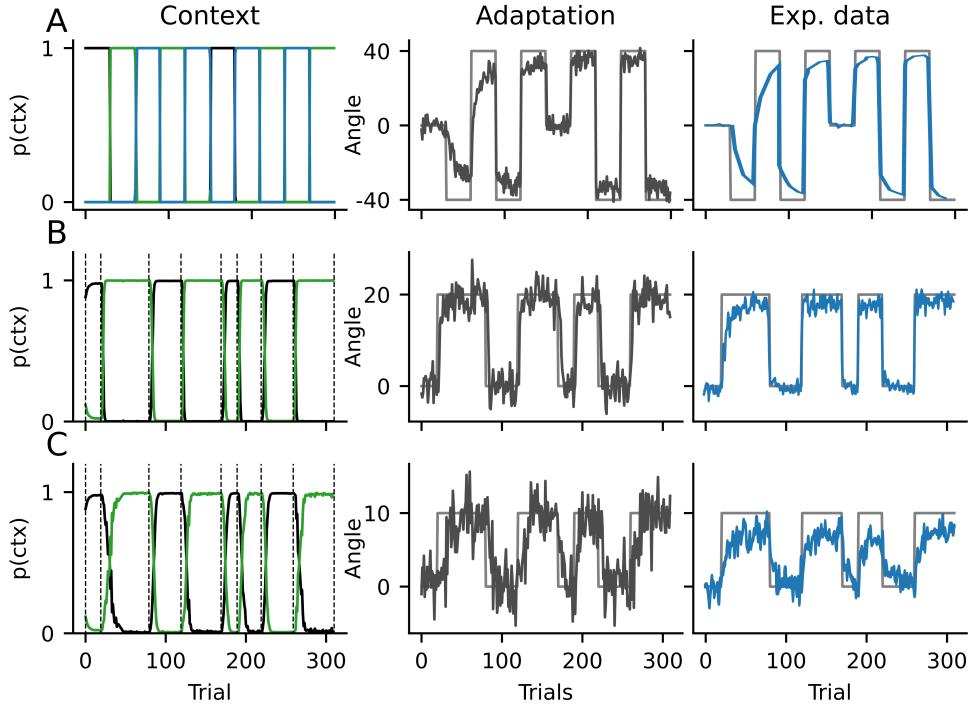


Figure 2. Savings and de-adaptation. Data from our simulations (first and second columns) compared to data adapted from figure 2A by Kim et al. (2015) and figure 4A from Oh and Schweighofer (2019) (last column). Experimental data was, in all three experiments, averaged across all participants; in our simulations, a single simulation is shown. In the first column, the simulated context over inference is represented by the posterior probabilities over all available contexts. Each color (black, blue, green) represents a different context, with black always representing the baseline (i.e. no adaptation). Vertical, dashed lines represent switches in the real context. In the second and third columns, the black line represents the adaptation (i.e. response) displayed by the agent as a function of trial number. The thin gray lines represent the optimal adaptation, i.e. the size of the true visuomotor rotation during the task. In all panels, the x-axis represents trial number, from 0 to 300. (A) Experiment by Kim et al. (2015) with two visuomotor rotations (-40 and 40 degrees), in addition to baseline, with all possible transitions between A, (-A) and O. Participants must adapt to the rotations during shooting movements, and the participant's response can be understood as the rotation of the participants' shooting movements to compensate for the task's rotation. For clarity, both experimental and simulated results are shown only up to trial 300, of the original 600. (B) An experiment by Oh and Schweighofer (2019) similar to (A), but the contexts were not cued and only one context, with an adaptation of 20 degrees, is introduced. O-A and A-O transitions (i.e. adaptation and de-adaptation) can be observed. Blue and black lines are as in A. (C) Same experiment as (B) but with a 10 degree adaptation.

230 2C), switching happens more slowly, with adaptation lagging behind the switches in the
 231 real context, and slowly catching up. As can be seen in the left panels in Figure 2B and
 232 2C, the same model parametrization produces fast, accurate switches when the adaptation
 233 is large (B), and slow, noisy switches when it is low (C). This difference is explained in
 234 our simulations in terms of the size of the adaptation in relation to observation noise: as
 235 the adaptation is smaller (10 degrees), it becomes more difficult to distinguish errors made
 236 by incorrectly inferring the context from the noise due to trial-to-trial variation in motor
 237 output. Because of this, the model requires more evidence (i.e. more trials) to infer a switch
 238 in contexts.

239 Note that the results from our simulations from Oh and Schweighofer (2019) and from
 240 Kim et al. (2015) include both savings (O-A transitions) and de-adaptation (A-O transi-
 241 tions), both of which display the same characteristics and are explained by the same
 242 mechanism.

243 **Uncertainty over contexts affects action selection.** As with learning, action
 244 selection is affected by context inference. If the identity of the current context is known, the
 245 forward model for this context is used to select the current action. However, if uncertainty
 246 over the context exists, the selected action is influenced by all the possible contexts, with a
 247 weight directly related to how likely each one of those contexts is (see Equation 5).

248 Experimental evidence supporting this view can be found in experiments with context
 249 switching. For example, Davidson and Wolpert (2004) reported a curl-force experiment in
 250 which participants had to switch from 3A to A in one group, with a block sequence A-3A-A-
 251 3A, and from -A to A in another group, with a block sequence A-(-A)-A-(-A). After A and
 252 3A (or -A in the other group) had been learned in the first two blocks, the authors found
 253 that the switch from 3A to A was faster than that from -A to A. The authors interpreted
 254 this as evidence that switching between adaptations happens more quickly if it is in the
 255 same direction as the current adaptation (e.g. both counter-clockwise), and more slowly if
 256 they are in the opposite direction (e.g. clockwise to counter-clockwise).

257 Under the COIN model, the asymmetry is caused by the existence of the baseline con-
 258 text, which has a non-zero probability $p(\zeta_O|s_t\dots)$. When a new block of trials starts (e.g.
 259 in the transition from 3A to A), a switch is inferred by the model (given feedback after the
 260 first trial) and ζ_O becomes more likely (given that ζ_{3A} has been ruled out). Therefore, in
 261 these first trials, action selection has a component guided by the baseline model, in which
 262 no extra compensatory force is applied, effectively “pulling” adaptation towards zero (no
 263 compensatory force). In the first group, this initial pull towards zero accelerates the trans-
 264 sition towards A because $3A > A > 0$, but in the second group, it slows down the switch
 265 because $A > 0 > -A$.

266 We simulated data with the model fitting the experimental structure in Davidson and
 267 Wolpert (2004). We show the results in Figure 3A, alongside the experimental results from
 268 Davidson and Wolpert (2004). It can be seen that the agent exposed to the -A context
 269 shifts back to A more slowly than the one exposed to 3A, qualitatively reproducing the
 270 data from Davidson and Wolpert (2004).

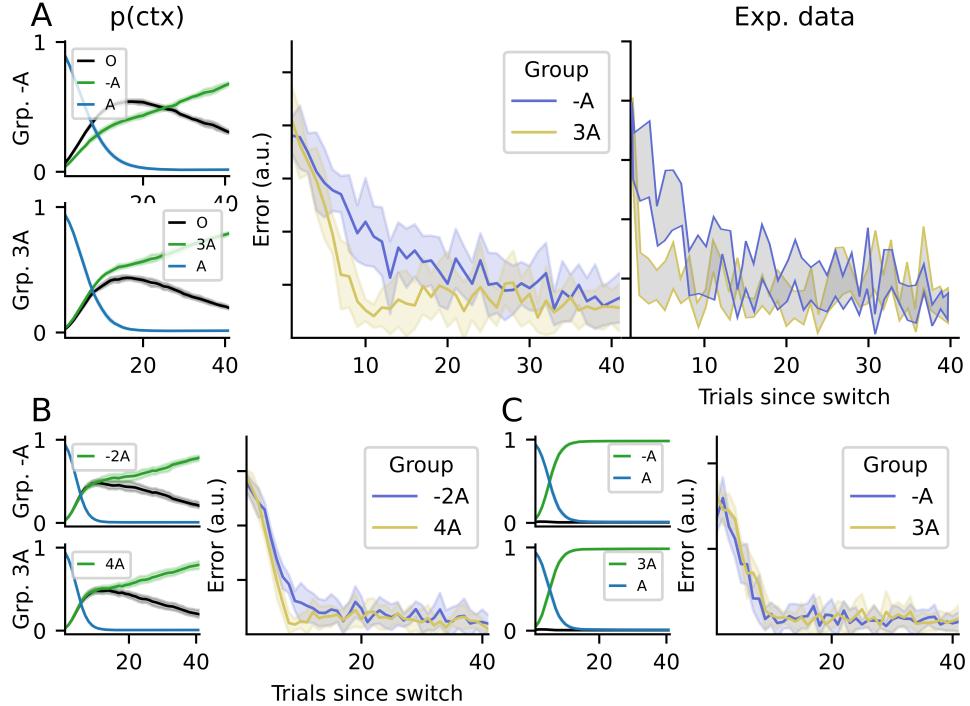


Figure 3. Motor error when switching back to a previously-learned adaptation. (A) Experimental results from Davidson and Wolpert (2004) and simulations with the COIN model are shown. In the first column, each panel represents context inference for one group of participants (top: group A; bottom: group 3A), with each line representing the posterior probability of a context (black for the baseline O). The second column represents the error made by our simulated agent after returning to the previously-learned context, with blue and yellow representing groups -A and 3A, respectively. The last panel represents the same data, from the Davidson and Wolpert (2004) experiment. All panels share the x-axis, representing the number of trials elapsed since the switch to the new context. All simulations were executed eight times per group, following the number of participants in the experiments; shaded areas represent the standard deviation across these eight simulations. (B) Simulated results for an experiment similar to Davidson and Wolpert (2004), but changing the contexts seen by the two groups from -A to -2A for the first group, and from 3A to 4A for the second group. The panels follow the same structure as (A), without the last panel for experimental results. (C) Simulations for an experiment in which the baseline context has been removed altogether.

271 To confirm our hypothesis, we simulated variants of the experiments in which the COIN
272 model predicts that the difference between groups disappears. First, in Figure 3B, we
273 simulated an experiment in which the contexts have more extreme adaptations, making
274 them more different from baseline than in the Davidson and Wolpert (2004) experiments.
275 To do this, one group adapts in a $O - A - (-2A)$ paradigm, while the other group adapts
276 in a $0 - A - 4A$ paradigm. As in the original experiment, the second contexts ($-2A$ for
277 one group, $4A$ for the other) are equally spaced from the first context. However, given the
278 larger distance from baseline, the baseline context has a much lower attribution when the
279 switch occurs compared to the original experiment. This change makes both simulated
280 groups infer the correct context almost equally quickly, making the difference between
281 their errors much smaller compared to the original experiment. Furthermore, we simulated
282 an experiment with an identical structure to that of Davidson and Wolpert (2004), but
283 eliminated the baseline context from the agent. The results can be seen in Figure 3C,
284 where the switches between contexts are made identically by the two groups. We discuss
285 possible implementations of such an experiment in the Discussion section, alongside with
286 other predictions made by the model.

287 **Action selection in error-clamp blocks.** During error-clamp blocks at the end
288 of block sequences, participants' behavior can be divided in two phases: (1) Participants'
289 behavior is consistent with a previously-encountered context (called spontaneous recover in
290 O-A-B-E experiments, where behavior is consistent with A); this phase, when present, is
291 seen during the early trials of the E block. (2) A slow return to baseline, which can last as
292 long as hundreds of trials (Brennan & Smith, 2015). However, the direction of adaptation
293 during the first phase, its duration, the delay before it is observed, the speed of the return to
294 baseline and the final asymptote of the response vary greatly depending on the experiment
295 (Brennan & Smith, 2015; Shmuelof et al., 2012; Smith et al., 2006; Vaswani & Shadmehr,
296 2013).

297 In this section, we show how context inference can explain these different parameters
298 of behavior by changing the way contextual cues mislead participants' context inference,
299 which in turn influences action selection.

300 This can be seen for example for Vaswani and Shadmehr (2013), who studied in de-
301 tail human behavior during an error-clamp block in a shooting movement paradigm with
302 a mechanical arm. The authors found that during an E block at the end of each experi-
303 ment, there was a lag of a few trials (depending on participant) before their motor behavior
304 changed from that of the previous block. After that, the exerted force slowly dropped to-
305 wards zero throughout tens of trials, but never reaching values around zero. Participants
306 were divided into four groups, each of which going through a different block sequence: (1)
307 A-E, (2) O-A-E, (3) (-A/2)-A-E, and (4) (-A)-E. No pauses were made during the experi-
308 ment nor were there any contextual cues, so transitions between blocks were not signaled
309 to participants. However, because context inference integrates information from different
310 sources, many experiments in which no intentional, overt contextual cues are available in-
311 deed contain contextual information that the participant can use to infer the context. For
312 example, proprioceptive signals provide contextual information (Dizio & Lackner, 1995;
313 Shadmehr & Mussa-Ivaldi, 1994). The sudden appearance of motor errors can itself be a

314 cue for contextual change (Herzfeld et al., 2014) and even a pause between two trials could
 315 suggest a change in context (Ethier et al., 2008).

316 In Figure 4A, we show data simulated with the COIN model, following the parameters
 317 of the experiment by Vaswani and Shadmehr (2013), and in Figure 4B we show the exper-
 318 imental plots adapted from Vaswani and Shadmehr (2013). The displayed adaptation is
 319 shown during the E trials for the three experimental groups in the experiment. It can be
 320 seen that group 1.3 (i.e. the participants who had learned in the -A/2 context in addition
 321 to A) more quickly recognized a change in context and lowers the force applied on the
 322 mechanical handle, as can be seen in the experimental data.

323 In Figure 4C, the inference over context is shown for each group separately. Context
 324 inference works reliably until the error-clamp trials start, which do not correspond to any
 325 of the known contexts. This causes the agent to infer the combination of some of the known
 326 contexts that best fits the observations. Depending on the contexts previously learned by
 327 the agent: groups 1.1 and 1.4 display the same behavior, where the previous context (A
 328 and -A, respectively) slowly dwindle. These agents will slowly lower the force applied. In
 329 contrast, group 1.3 has learned the additional -A/2 context, which has a non-zero posterior
 330 probability during E trials, pushing the agent’s adaptation force more quickly towards zero.
 331 Group 1.2 behaves similarly to 1.1, with the exception that the baseline context, which was
 332 recently seen, plays a bigger role during E trials, making the agent reduce its force during
 333 E trials slightly more quickly than groups 1.1 and 1.4.

334 Context inference also explains the variability in the lag before adaptation starts to drop
 335 to zero after the E block starts. In the model, this lag is due to a period in which context
 336 inference has not “caught on” to the change of context; during this period, behavior remains
 337 consistent with that of the previously-observed block, as can be seen in the experimental
 338 data as well. Furthermore, variability in the lag between and within groups is explained by
 339 perceptual noise, which directly affects context inference. To show these effects, we show in
 340 Figure 4D the drop in the inferred probability of the previous context for each simulated run
 341 (one line per run, 10 runs per group, all groups). The start and speed of the drop depend
 342 on the run (i.e. the participant), reproducing the different lags observed in experimental
 343 data.

344

Discussion

345 We showed that context inference as an active, continuous process, can explain many
 346 behavioral phenomena observed experimentally. In particular, we showed that the effects
 347 of the presence and reliability of contextual cues, as well as observation noise, can cause
 348 behavior that can be observed during context switching, as well as during times in which
 349 context inference is hindered, as is the case during error-clamp trials in many experiments.

350 To do this, we selected representative experimental studies that show the well-established
 351 effects of savings, quick de-adaptation, spontaneous recovery and the effects of sensory cues.
 352 Using the COIN model introduced by Heald et al. (2021), we showed how each of these effects

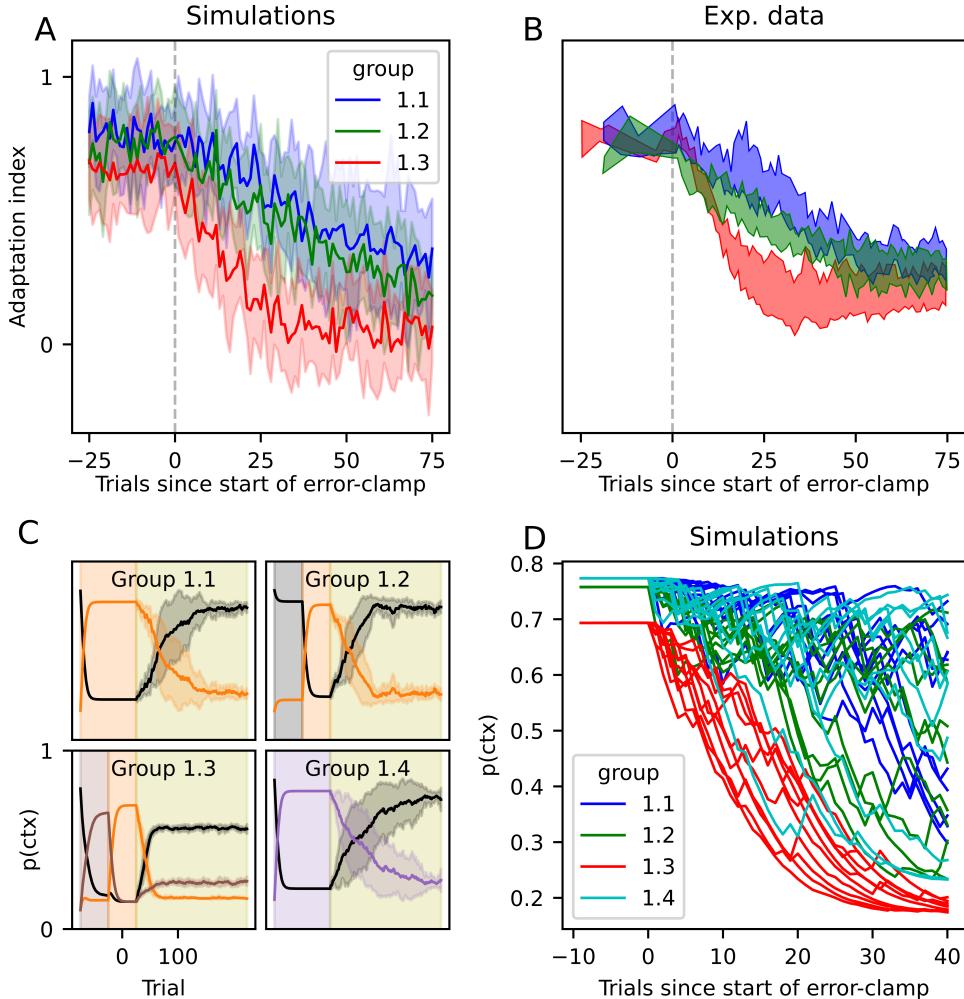


Figure 4. Adaptation during error clamp trials. (A) Simulated adaptation during the error-clamp trials for the three groups of participants in Vaswani and Shadmehr (2013), using the same colors. The groups differ in the sequence of adaptations: 1.1 performed an A-E sequence; 1.2, O-A-E; 1.3, (-A/2)-A-E; and 1.4, (-A)-E. Following Vaswani and Shadmehr (2013), group 1.4 is not shown in A and B, as their behavior is identical to group 1.1. The solid line is the average across 10 runs (i.e. a group of 10 simulated participants) and the shaded area represents the standard deviation. The vertical dashed line is the start of the error-clamp trials. (B) Corresponding experimental data adapted from figure 2C by Vaswani and Shadmehr (2013). (C) Simulations: Inference over the current context, where contexts are color coded: black for baseline, orange for the counter-clockwise force, purple for the clockwise force and brown for counter-clockwise force with half strength. The lines represent the posterior probability of each context in every trial, while the background color represents the true context. An olive-colored background represents error-clamp trials. As in (A), solid lines represent the average across all runs and shaded areas represent the standard deviation. (D) Simulations: Visualization of the lag before a change in context is detected by the agent during the E trials. Each line represents one run (10 runs per group).

353 can be explained by the dynamics of context inference, which integrates all the available
354 information (e.g. sensory cues, workspace location, reward and endpoint feedback), in some
355 cases throughout many trials.

356 With this, we expanded on previous works that introduced the idea that context in-
357 ference is a process that informs and is informed by motor adaptation by showing that
358 it explains behavioral phenomena that had previously required different specific, ad-hoc
359 mechanisms outside of contextual motor adaptation.

360 **Further experimental evidence**

361 In many cases, the context is not directly observable and context inference takes the
362 form of an evidence-accumulating process that can take any amount of time to be sure of
363 the context. It is in these cases where the effects of context inference are most noticeable.
364 While many experiments exist that give probabilistic contextual information (e.g. Behrens,
365 Woolrich, Walton, & Rushworth, 2007; Nassar, McGuire, Ritz, & Kable, 2019; Scholz &
366 Schöner, 1999), evidence accumulation is not limited to these explicit cases. Indeed, as we
367 noted in the Results section, many experiments inadvertently include partial contextual
368 information used by participants.

369 The most direct secondary contextual information comes in the form of reward and end-
370 point feedback. For example, participants may be told whether they obtained the desired
371 reward at the end of a trial and are shown the end point of their movement. When partic-
372 ipants observe an unexpectedly large error, they can infer that the inferred context might
373 be incorrect. This is the case of the experiments by Oh and Schweighofer (2019) shown
374 in Figure 2B-C: if the adaptation is high, changes in context produce errors much larger
375 than those of motor variability, and a context switch is easily and immediately identified;
376 if adaptation is low, the errors produced by context switching are closer in magnitude to
377 motor variability and evidence accumulation is necessary.

378 The same rationale explains the results by Herzfeld et al. (2014), as was shown by Heald
379 et al. (2021): motor learning, which in the COIN model is modulated by context inference,
380 is minimal for errors close to 2 and -2 (see their figure 2E). This is because an error of
381 2 or -2 signals that the participant incorrectly identified the context (as adaptation has
382 a magnitude of 1). Additionally, as was shown by Heald et al. (2021), context inference
383 explains the modulation of learning rate by the volatility of the environment observed by
384 Herzfeld et al. (2014).

385 A subtler source of information can be found in long pauses between blocks of adapta-
386 tion trials, after which an unprompted partial return to baseline has been observed Ethier
387 et al. (2008). This can be explained by context inference, as a long pause could prompt par-
388 ticipants to infer that a switch had occurred, prompting participants to rely on their belief
389 of the underlying probability of observing any of the known contexts, which is dominated
390 by the previously observed context A, but now includes a component of the baseline O, as
391 it is the most common one in everyday life.

392 Error-clamp (E) trials present another insight. If error is kept at zero, one could assume
393 that participants would continue doing what they were doing before, as there is no reason
394 (no observed error) to infer a change in context. However, this is almost never the case (e.g.
395 Ethier et al., 2008; Forano & Franklin, 2020; Pekny, Criscimagna-Hemminger, & Shadmehr,
396 2011; Scheidt, Reinkensmeyer, Conditt, Rymer, & Mussa-Ivaldi, 2000; Smith et al., 2006;
397 Vaswani & Shadmehr, 2013). Instead, participants slowly reduce their adaptation, often
398 displaying spontaneous recovery (e.g. Smith et al., 2006). Context inference provides a prin-
399 cipled account of this behavior: the natural variability in participants' behavior lead them
400 to expect errors, which clashes with the observed zero error. This prompts participants to
401 re-evaluate their inferred context, which can partially activate a previously-observed con-
402 text, as we showed in Figure 4. Pekny et al. (2011) found similar results, demonstrating
403 that the duration of the previously-observed adaptation block also affects behavior in the E
404 block. Additionally, Criscimagna-Hemminger and Shadmehr (2008) showed that introduc-
405 ing long periods before the E block begins lowers the initial force that participants exerted
406 on the mechanical arm during the E block; longer periods of time make context inference
407 revert to the prior expectation that a new baseline block begins, because participants are
408 free to move their arm about during the pause.

409 In our account, if all information indicating a change in context is removed from the
410 experiment, participants would continue to behave as they were in the previous block.
411 Evidence for this can be seen in experiments 2 and 3 by Vaswani and Shadmehr (2013),
412 where participants were shown random errors during E trials, with a variance matching
413 that of previously observed motor commands. The authors showed that by matching the
414 errors expected by participants, they eliminated the slow tapering-off observed in most E
415 blocks.

416 Model predictions

417 The basic principle behind the results we presented is that the COIN model describes
418 a process that develops over time and that carries with it uncertainty. This uncertainty
419 affects learning and behavior during motor adaptation, effecting phenomena that are directly
420 observable during behavioral experiments. In the following, we discuss several testable
421 predictions that are direct consequences of the model.

422 For the model predictions discussed below, it is important to keep in mind that different
423 contextual cues are not equally effective at separating motor responses during learning and
424 switching Howard, Ingram, Franklin, and Wolpert (2012); Howard, Ingram, and Wolpert
425 (2010); Imamizu et al. (2007). Because of this, the model predictions hinge on selecting the
426 adequate type of contextual information that maximally helps the participants select the
427 appropriate motor response.

428 **Error-clamp as a known context.** The inclusion of reliable sensory contextual cues
429 (e.g. lights whose color uniquely identify a context) makes switching immediate, as in the
430 experiments by Kim et al. (2015). We expect that the same effect would be observed in
431 error-clamp trials. If the E block is learned by participants during training, it might still

432 be difficult for them to infer that an E block has started, which would create delays similar
433 to those in Figure 4. However, the model predicts that if a visual cue is introduced that
434 identifies the E block, participants would immediately switch to their baseline behavior, no
435 longer displaying an adapted response, lag, nor the slow return to baseline. This immediate
436 switch in the presence of contextual cues would persist even if endpoint feedback is
437 manipulated as Vaswani and Shadmehr (2013) did.

438 Note that the original COIN specification includes a component to learn new contexts.
439 However, this component works exclusively by creating new contexts in which the forward
440 models take the same form but have different parameter values. New mechanisms would
441 be needed to allow the COIN model to create contexts in an online fashion that operate in
442 an essentially different manner, as is the case of error-clamp trials, in which participants'
443 responses do not affect the outcome and motor commands are issued based on criteria not
444 directly related to the goal of the task (e.g. energy minimization or comfort maximization).

445 **Interference effects during context switching.** As discussed in the Results section,
446 the effect observed by Davidson and Wolpert (2004) is explained by the model as an effect
447 of slow context inference, instead of being a direct interference at the level of learning.
448 As shown in Figure 3B-C, the context inference account predicts that this effect would
449 disappear if all contexts were significantly different from baseline, such that the baseline
450 context never explains the observations. Removing the baseline context from a participant's
451 context inference might be experimentally unfeasible, but other possibilities include making
452 all adaptations bigger (e.g. bigger angles, stronger forces), and including contextual cues
453 that rule out the baseline context. In the opposite direction, the model predicts that if
454 all adaptations are smaller (i.e. closer to baseline), the differences between the two groups
455 would increase.

456 **Reducing the effect of volatility on learning.** Experiments (Heald et al., 2021;
457 Herzfeld et al., 2014) have shown an effect of the volatility of the environment (i.e. un-
458 predictable switching between contexts) on measured learning rate. The model predicts
459 that this effect would be greatly reduced if reliable contextual cues were introduced: if a
460 participant can infer the context of the current trial before any decision or observation has
461 occurred, the learning rate would not be affected by the volatility of the environment. Heald
462 et al. (2021) showed that the COIN model explains this change in terms of the Kalman gain
463 and the posterior probability over contexts (see their equation 14).

464 If this prediction is confirmed, the model would additionally suggest that human par-
465 ticipants do not revisit the learned adaptation of the previous trial when a new observa-
466 tion comes in. To see this, consider the following scenario from the experiments by Herzfeld et
467 al. (2014): at trial t , the true context was B but the participant inferred context A, issued a
468 motor command consistent with context A and then observed the outcome at $t + 1$. When
469 the outcome is observed, it becomes clear to the participant that the context was B. Does
470 the participant update the internal model of A or of B? According to the model, partici-
471 pants incorrectly update A and, upon learning of their mistake at trial $t + 1$, do not revert
472 this update. If this were not the case, the volatility of the environment would have no effect
473 even without contextual cues, as the context at trial t can almost always be identified at

474 trial $t + 1$.

475 **Multi-source integration.** The model also predicts an effect reminiscent of multi-
 476 sensory integration (Ernst & Banks, 2002): in order to integrate contextual information
 477 from conflicting sources (e.g. probabilistic visual cues and noisy endpoint feedback), the
 478 weight placed on a source increases with its reliability. Such integration would manifest
 479 itself in experiments in which observations are noisy, as in the experiments by Kording and
 480 Wolpert (2004), in which the position of the finger was obscured and instead participants
 481 are shown a blurry cursor which was sometimes shifted from its real position. If the added
 482 observation noise gives evidence for a particular context (the true underlying context or an-
 483 other one) and a visual cue gave partial information for another context, the participants’
 484 behavior would be more consistent with the most reliable source of contextual information.

485 **Conclusions**

486 The results we presented in this work indicate that several well-established behavioral
 487 phenomena observed across different motor adaptation experiments can be explained by the
 488 uncertainty in context inference and its effects on learning and action selection. Together
 489 with the results by Heald et al. (2021), these results suggest new venues of investigation for
 490 future works in motor adaptation and context-dependent behavior.

491 **Methods**

492 **The COIN model**

493 In this work, we used the recently-introduced COIN model (Heald et al., 2021), adapted
 494 to the experiments that we covered in our simulations. In this section, we give a brief
 495 introduction to the COIN model and, in the subsequent subsection, describe how we adapted
 496 the model to the experimental tasks. For a full description of the model, refer to Heald et
 497 al. (2021).

498 **Generative model.** At each trial t , the agent infers both the context and the context-
 499 dependent adaptation (e.g. the parameters of the force field in mechanical-arm experi-
 500 ments). The context is represented by a latent, categorical variable ζ_t :

$$p(\zeta_t | \zeta_{t-1}, \pi_{\zeta_{t-1}}) = \text{Discrete}(\pi_{\zeta_{t-1}}) \quad (1)$$

501 where $\pi_{\zeta_{t-1}}$ is the transition probability vector from context ζ_{t-1} to all other contexts. The
 502 contextual cues (when present in an experiment) are assumed to be drawn depending on
 503 the context following:

$$p(q_t | c_t, \Phi) = \text{Discrete}(\Phi_{\zeta_t}) \quad (2)$$

504 where Φ_{ζ_t} is the probability vector with which the contextual cue q_t is shown to the agent
 505 in context ζ_t . As pointed out by Heald et al. (2021), both Φ and π are in principle infinite,
 506 but a task-relevant finite set can be used instead.

507 The context-dependent adaptation is represented by the latent variable $x_{\zeta,t}$ and assumed
 508 to arise from an autoregressive process AR(1), with a stationary Gaussian distribution of
 509 unknown mean and variance:

$$p(x_{\zeta,t}) = \mathcal{N}(\mu_{\zeta,x}, \sigma_{\zeta,x}) \quad (3)$$

510 Note that $\mu_{\zeta,x}$ and $\sigma_{\zeta,x}$ are parametrized by the parameters of the AR(1) process, namely
 511 $\mu_{\zeta,x} = d_{\zeta}/(1 - a_{\zeta})$ and $\sigma_{\zeta,x} = \sigma_q/1 - a_{\zeta}^2$, where σ_q is a free parameter of the model which
 512 is not context dependent.

513 Observations take the form of state feedback (e.g. the position of the cursor on the
 514 screen in visuomotor rotation tasks), given by:

$$y_t = x_{\zeta,t} + \nu_t \quad (4)$$

515 where ν_t is a zero-mean Gaussian noise term with unknown standard deviation σ_r , which
 516 is a free parameter of the model.

517 Action selection (i.e. motor output u_t) is done via the weighted mean of $x_{j,t}$:

$$u_t = \sum_j p(\zeta_{j,t}|...)x_{j,t} \quad (5)$$

518 To include motor noise (independent from estimation uncertainty), as well as carry over the
 519 uncertainty over $x_{j,t}$, we instead sample motor commands from a Gaussian centered on this
 520 mean, with a standard deviation σ_u , which is a free parameter of the model.

521 **Using the model.** The free parameters of this model can be fitted to participants'
 522 data, as was done by Heald et al. (2021). In this work, we instead chose values for these
 523 parameters to show that the model is capable of explaining the experimental phenomena in
 524 the Results section. Additionally, by fixing these parameters the agent is able to perform
 525 exact Bayesian inference at each trial using conjugate priors, replacing the MCMC approach
 526 used by Heald et al. (2021) due to the mathematical intractability of the full formulation.
 527 This, however, does not significantly change the model and was done purely for computa-
 528 tional efficiency. In this section, we describe how we fixed parameters and the procedure
 529 for Bayesian inference.

530 As explained above, context is assumed to be a discrete variable which evolves as a
 531 Markov process. The transition matrices π were generated via a Dirichlet process, with
 532 parameters that can be inferred from participant data (α and κ in Heald et al. (2021)). For
 533 a fixed value of these parameters, the transition matrices also become fixed. In our simula-
 534 tions, we set the probability of self-transitioning (denoted p_{ζ}) depending on the experiments
 535 (see below), to numbers that match the experimental setup of each study.

536 Contextual cues are assumed by the agent to be sampled from a distribution that de-
 537 pends on the current context. This is done through a set of cue probability vectors that are
 538 generated via a parametric distribution, whose parameters are fitted to participants' data.
 539 Because the experiments we simulate do not include probabilistic or deceiving cues, contex-
 540 tual cues, when present, unequivocally reflect the current context, i.e. $p(q_t = i|c_t = j) = d_{ij}$,
 541 where d_{ij} is the Kronecker delta, equaling one when $i = j$, zero otherwise.

Finally, we chose a different parametrization for the priors over the hidden variables $x_{j,t}$, using the mean μ_x and standard deviation σ_x directly instead of the AR(1) a and d parameters used by Heald et al. (2021). In what follows, we dropped the j dependency for clarity. This parametrization, in conjunction with the fixed parameters outlined above, allows us to set priors over $\mu_{\zeta,x}$ and $\sigma_{\zeta,x}$ that enable exact inference over the latent variables:

$$\mu_x, \sigma_x \sim \mathcal{N}\mathcal{G}(\mu_0, \nu_0, \alpha_0, \beta_0) \quad (6)$$

with free parameters μ_0 , ν_0 , α_0 and β_0 , which we fixed for each experiment separately. Because x is context-specific, so are these parameters. This formulation comes with four free parameters (i.e. the hyper-priors $\mu_{0,i}, \nu_{0,i}, \alpha_{0,i}, \beta_{0,i}$), in accordance with the original formulation (note that Heald et al. (2021) fixed the mean of the priors for b to zero). While the two formulations are not mathematically identical, the effects of the hyper-priors for both are the same; we discuss these effects in the next section.

Because the likelihood function $p(y_t|x_t, \dots)$ is Gaussian, this choice of priors allows us to calculate the update equations as follows:

$$\begin{aligned} \mu_{\phi,i}^{(t)} &= \frac{\nu_{\phi,i}^{(t-1)} \mu_{\phi,i}^{(t-1)} + q(\zeta_i) s_t}{\nu_{\phi,i}^{(t-1)} + q(\zeta_i)} \\ \nu_{\phi,i}^{(t)} &= \nu_{\phi,i}^{(t-1)} + q(\zeta_i) \\ \alpha_{\phi,i}^{(t)} &= \alpha_{\phi,i}^{(t-1)} + q(\zeta_i)/2 \\ \beta_{\phi,i}^{(t)} &= \beta_{\phi,i}^{(t-1)} + \frac{q(\zeta_i) \nu_{\phi,i}^{(t-1)}}{\nu_{\phi,i}^{(t-1)} + q(\zeta_i)} \frac{(s_t - \mu_{\phi,i}^{(t-1)})^2}{2} \end{aligned} \quad (7)$$

where s_t represents the observations, in the form of the error between the observed and expected outcomes of the motor command. Note that the effect of the evidence (i.e. observations) on the inference over the context-dependent hidden states is gated by the probability of each context $p(\zeta_i)$, as in (Heald et al., 2021, supplementary materials).

Model parameters. Table 1 lists all the parameter values that we used during our simulations. The parameters are divided into two categories: (1) task parameters, which encode the way we simulated the experimental design; (2) agent parameters, which correspond to the free parameters listed in the previous section. The variable names for the model parameters are given in the “Var” column, corresponding to the variables in the previous section. The values are divided into experiments and, within experiments, into the different groups or conditions that we simulated.

We estimated the task parameters from the information provided in their respective publications; when direct information was not provided, we estimated it from the reported results; these estimations are not exact, but function as a proof of concept. Agent parameter values are held constant for the different conditions or groups for each experiment, except those parameters that are expected to vary across conditions.

	Var	Description	Kim (2015)		Oh (2009)		Davidson (2004)		Vaswani (2013)		
			Exp. 1	Exp. 2	Grp. 3A	Grp. -A	Grp. 1	Grp. 2	Grp. 3		
Task pars.	Contextual cues	Yes				No					
	x_j^*	Adaptation sizes	0, 40, -40	0, 20	0, 10	0, 4, -4	0, 4, 12	1	0, 1	-0.5, 1	
	σ_r^*	Adaptation noise	0.01		1		0.5		0.01		
	σ_r	Obs. noise	3		1.5		0.1		0.01		
Agent pars.	p_ζ	Context self-transition	0.9		0.98		0.98		0.9	0.8	
	μ_0	Hyper priors	0, -1, 1		0, 0		0, 4, -4	0, 4, 12	0, 1	0, 1, -0.5	
	ν_0		1e4, 10, 10		0, 0		1e4, 0.5, 0.5		1e4, 1	1e4, 1, 1	
	α_0		25e4, 0.25, 0.25		22e4, 2.2		33e4, 33, 33		5e5, 5	15e5, 5, 5	
	β_0		1e5, 2, 2		1e5, 20		1e5, 200, 200		1e5, 2	1e5, 2, 2	
	σ_u	Motor noise	0.001			2			0.17		
	σ_r	Obs. noise	3		3.5		2.5		0.1		

Table 1

Model and simulation parameters.

569 The context-dependent hyper-priors $\{\mu_0, \nu_0, \alpha_0, \beta_0\}$ effect a learning rate and, as such,
570 were set such that the learning rate for the baseline context is nearly zero, following the
571 assumption that participants will not change the way they perform these movements outside
572 of the lab. The values for contexts outside of baseline were set identically within each
573 experiment.

574 The star notation (e.g. x_j^*) denotes the real value used in the simulation of the task,
575 which may be different from that assumed by the agent.

576 For the simulations in Figure 1, the parameters were set as in the experiments by
577 Davidson and Wolpert (2004), with two exceptions: (1) the cue noise, which is set to the
578 values of 0, 0.003 and 0.33, for the low, medium and high values, respectively; and (2) the
579 agent’s observation noise σ_r , with values of 0.5, 1 and 2.

580 **Interpreting the hyper-parameters.** μ determines the initial estimate of the adap-
581 tation, in the same units as the necessary adaptation. ν encodes how stable this hyper-prior
582 is: higher values (e.g. 10,000) all but guarantee that the hyper-prior μ will not change its
583 value after observations; In principle, enough evidence should still modify it, but that would
584 not happen during an experiment. Smaller values (i.e. ~ 1) make μ follow evidence more
585 freely. Note that as more observations are accumulated, ν becomes bigger and bigger,
586 stabilizing the value of μ .

587 The hyper-parameters α and β have a more complex effect. Note that the mean of a
588 gamma distribution is $1/(\alpha\nu)$; this mean is being used as the standard deviation of a Gaus-
589 sian by the rest of the agent, which makes it an important measure of uncertainty. While
590 setting the default hyper-parameters, the values used are $\alpha = 0.5/\sigma_0$ and $\beta = 0.5$, where σ_0
591 is the *a priori* estimate of the standard deviation of the force exerted by the environment,
592 which controls the initial learning rate. This makes the initial standard deviation equal σ_0 ,
593 which makes it consistent with the fixed-force model. The 0.5 values ensure that uncer-
594 tainty is large at the beginning and is greatly reduced during the experiment, but never to
595 a point where it is so small that it makes trial-to-trial variation in the environment surpris-
596 ing. Changing this 0.5 would make the standard deviation change more quickly, making the
597 model more or less precise in its predictions, independently of the volatility of the mean of

598 the adaptation (via μ).

599 The baseline model defaults to different values that make it a lot more stable. The
600 hyper-standard deviation of the mean is set to 10,000, which makes the mean entirely
601 stable during the duration of the experiment. The values of α and β are fixed regardless of
602 σ_0 such that the standard deviation is 0.001 (compared that to the size of the adaptations
603 in mechanical arm experiments, around 0.0125), and the hyper-parameters of the standard
604 deviation are stable during the experiment.

605

Acknowledgment

606 Funded by the German Research Foundation (DFG, Deutsche Forschungsgemeinschaft)
607 as part of Germany’s Excellence Strategy – EXC 2050/1 – Project ID 390696704 – Cluster
608 of Excellence “Centre for Tactile Internet with Human-in-the-Loop” (CeTI) of Technische
609 Universität Dresden.

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References

- 611 Behrens, T. E. J., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. S. (2007, September).
612 Learning the value of information in an uncertain world. *Nature Neuroscience*, 10(9), 1214–
613 1221. doi: 10.1038/nn1954
- 614 Brashers-Krug, T., Shadmehr, R., & Bizzi, E. (1996, July). Consolidation in human motor memory.
615 *Nature*, 382(6588), 252–255. doi: 10.1038/382252a0
- 616 Brennan, A. E., & Smith, M. A. (2015, June). The Decay of Motor Memories Is Independent of
617 Context Change Detection. *PLOS Computational Biology*, 11(6), e1004278. doi: 10.1371/jour-
618 nal.pcbi.1004278
- 619 Criscimagna-Hemminger, S. E., & Shadmehr, R. (2008, September). Consolidation Pat-
620 terns of Human Motor Memory. *Journal of Neuroscience*, 28(39), 9610–9618. doi:
621 10.1523/JNEUROSCI.3071-08.2008
- 622 Davidson, P. R., & Wolpert, D. M. (2004, November). Scaling down motor memories:
623 De-adaptation after motor learning. *Neuroscience Letters*, 370(2-3), 102–107. doi:
624 10.1016/j.neulet.2004.08.003
- 625 Dizio, P., & Lackner, J. R. (1995, October). Motor adaptation to Coriolis force perturbations of
626 reaching movements: Endpoint but not trajectory adaptation transfers to the nonexposed
627 arm. *Journal of Neurophysiology*, 74(4), 1787–1792. doi: 10.1152/jn.1995.74.4.1787
- 628 Ernst, M. O., & Banks, M. S. (2002, January). Humans integrate visual and haptic information in
629 a statistically optimal fashion. *Nature*, 415(6870), 429–433. doi: 10.1038/415429a
- 630 Ethier, V., Zee, D. S., & Shadmehr, R. (2008, May). Spontaneous Recovery of Motor Mem-
631 ory During Saccade Adaptation. *Journal of Neurophysiology*, 99(5), 2577–2583. doi:
632 10.1152/jn.00015.2008
- 633 Forano, M., & Franklin, D. W. (2020, October). Timescales of motor memory formation in
634 dual-adaptation. *PLOS Computational Biology*, 16(10), e1008373. doi: 10.1371/jour-
635 nal.pcbi.1008373
- 636 Gandolfo, F., Mussa-Ivaldi, F. A., & Bizzi, E. (1996, April). Motor learning by field ap-
637 proximation. *Proceedings of the National Academy of Sciences*, 93(9), 3843–3846. doi:
638 10.1073/pnas.93.9.3843

- 639 Heald, J. B., Lengyel, M., & Wolpert, D. M. (2021, December). Contextual inference underlies the
640 learning of sensorimotor repertoires. *Nature*, *600*(7889), 489–493. doi: 10.1038/s41586-021-
641 04129-3
- 642 Herzfeld, D. J., Kojima, Y., Soetedjo, R., & Shadmehr, R. (2018, May). Encoding of error and
643 learning to correct that error by the Purkinje cells of the cerebellum. *Nature Neuroscience*,
644 *21*(5), 736–743. doi: 10.1038/s41593-018-0136-y
- 645 Herzfeld, D. J., Vaswani, P. A., Marko, M. K., & Shadmehr, R. (2014, September). A memory of
646 errors in sensorimotor learning. *Science*, *345*(6202), 1349–1353. doi: 10.1126/science.1253138
- 647 Howard, I. S., Ingram, J. N., Franklin, D. W., & Wolpert, D. M. (2012, September). Gone in 0.6
648 Seconds: The Encoding of Motor Memories Depends on Recent Sensorimotor States. *Journal*
649 *of Neuroscience*, *32*(37), 12756–12768. doi: 10.1523/JNEUROSCI.5909-11.2012
- 650 Howard, I. S., Ingram, J. N., & Wolpert, D. M. (2010, October). Context-Dependent Partitioning
651 of Motor Learning in Bimanual Movements. *Journal of Neurophysiology*, *104*(4), 2082–2091.
652 doi: 10.1152/jn.00299.2010
- 653 Huang, V. S., & Shadmehr, R. (2009, August). Persistence of Motor Memories Reflects
654 Statistics of the Learning Event. *Journal of Neurophysiology*, *102*(2), 931–940. doi:
655 10.1152/jn.00237.2009
- 656 Imamizu, H., Sugimoto, N., Osu, R., Tsutsui, K., Sugiyama, K., Wada, Y., & Kawato, M. (2007,
657 August). Explicit contextual information selectively contributes to predictive switching of
658 internal models. *Experimental Brain Research*, *181*(3), 395–408. doi: 10.1007/s00221-007-
659 0940-1
- 660 Kim, S., Ogawa, K., Lv, J., Schweighofer, N., & Imamizu, H. (2015, December). Neural Substrates
661 Related to Motor Memory with Multiple Timescales in Sensorimotor Adaptation. *PLOS*
662 *Biology*, *13*(12), e1002312. doi: 10.1371/journal.pbio.1002312
- 663 Kording, K. P., & Wolpert, D. M. (2004, January). Bayesian integration in sensorimotor learning.
664 *Nature*, *427*(6971), 244–247. doi: 10.1038/nature02169
- 665 Lee, J.-Y., & Schweighofer, N. (2009, August). Dual Adaptation Supports a Parallel Ar-
666 chitecture of Motor Memory. *Journal of Neuroscience*, *29*(33), 10396–10404. doi:
667 10.1523/JNEUROSCI.1294-09.2009
- 668 Marko, M. K., Haith, A. M., Harran, M. D., & Shadmehr, R. (2012, September). Sensitivity to
669 prediction error in reach adaptation. *Journal of Neurophysiology*, *108*(6), 1752–1763. doi:
670 10.1152/jn.00177.2012
- 671 Medina, J. F., Garcia, K. S., & Mauk, M. D. (2001, June). A Mechanism for Savings in the
672 Cerebellum. *Journal of Neuroscience*, *21*(11), 4081–4089. doi: 10.1523/JNEUROSCI.21-11-
673 04081.2001
- 674 Nassar, M. R., McGuire, J. T., Ritz, H., & Kable, J. W. (2019, February). Dissociable Forms of
675 Uncertainty-Driven Representational Change Across the Human Brain. *Journal of Neuro-
676 science*, *39*(9), 1688–1698. doi: 10.1523/JNEUROSCI.1713-18.2018
- 677 Oh, Y., & Schweighofer, N. (2019, November). Minimizing Precision-Weighted Sensory Prediction
678 Errors via Memory Formation and Switching in Motor Adaptation. *Journal of Neuroscience*,
679 *39*(46), 9237–9250. doi: 10.1523/JNEUROSCI.3250-18.2019
- 680 Pekny, S. E., Criscimagna-Hemminger, S. E., & Shadmehr, R. (2011, September). Protection and
681 Expression of Human Motor Memories. *The Journal of Neuroscience*, *31*(39), 13829–13839.
682 doi: 10.1523/JNEUROSCI.1704-11.2011
- 683 Scheidt, R. A., Dingwell, J. B., & Mussa-Ivaldi, F. A. (2001, August). Learning to Move Amid
684 Uncertainty. *Journal of Neurophysiology*, *86*(2), 971–985. doi: 10.1152/jn.2001.86.2.971
- 685 Scheidt, R. A., Reinkensmeyer, D. J., Conditt, M. A., Rymer, W. Z., & Mussa-Ivaldi, F. A. (2000,
686 August). Persistence of motor adaptation during constrained, multi-joint, arm movements.
687 *Journal of Neurophysiology*, *84*(2), 853–862. doi: 10.1152/jn.2000.84.2.853
- 688 Scholz, J. P., & Schöner, G. (1999, May). The uncontrolled manifold concept: Identifying con-
689 trol variables for a functional task. *Experimental Brain Research*, *126*(3), 289–306. doi:

- 690 10.1007/s002210050738
691 Shadmehr, R., & Brashers-Krug, T. (1997, January). Functional Stages in the Formation
692 of Human Long-Term Motor Memory. *Journal of Neuroscience*, 17(1), 409–419. doi:
693 10.1523/JNEUROSCI.17-01-00409.1997
694 Shadmehr, R., & Mussa-Ivaldi, F. A. (1994, May). Adaptive representation of dynamics during
695 learning of a motor task. *The Journal of Neuroscience: The Official Journal of the Society
696 for Neuroscience*, 14(5 Pt 2), 3208–3224.
697 Shmuelof, L., Huang, V. S., Haith, A. M., Delnicki, R. J., Mazzoni, P., & Krakauer, J. W. (2012, Oc-
698 tober). Overcoming Motor “Forgetting” Through Reinforcement Of Learned Actions. *Journal
699 of Neuroscience*, 32(42), 14617–14621a. doi: 10.1523/JNEUROSCI.2184-12.2012
700 Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006, June). Interacting Adaptive Processes
701 with Different Timescales Underlie Short-Term Motor Learning. *PLoS Biology*, 4(6). doi:
702 10.1371/journal.pbio.0040179
703 Vaswani, P. A., & Shadmehr, R. (2013, May). Decay of Motor Memories in the Absence of Error.
704 *Journal of Neuroscience*, 33(18), 7700–7709. doi: 10.1523/JNEUROSCI.0124-13.2013
705 Zarahn, E., Weston, G. D., Liang, J., Mazzoni, P., & Krakauer, J. W. (2008, November). Explaining
706 Savings for Visuomotor Adaptation: Linear Time-Invariant State-Space Models Are Not
707 Sufficient. *Journal of Neurophysiology*, 100(5), 2537–2548. doi: 10.1152/jn.90529.2008