

1 **Title:** A Synthesis of the Many Errors and Learning Processes of Visuomotor Adaptation

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3 **Running Title:** The Errors and Learning Processes of Visuomotor Adaptation

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11

12 **Abstract**

13 Visuomotor adaptation has one of the oldest experimental histories in psychology and neuroscience,
14 yet its precise nature has always been a topic of debate. Here we offer a survey and synthesis of recent
15 work on visuomotor adaptation that we hope will prove illuminating for this ongoing dialogue. We
16 discuss three types of error signals that drive learning in adaptation tasks: task performance error,
17 sensory prediction-error, and a binary target hitting error. Each of these errors has been shown to
18 drive distinct learning processes. Namely, both target hitting errors and putative sensory prediction-
19 errors drive an implicit change in visuomotor maps, while task performance error drives learning of
20 explicit strategy use and non-motor decision-making. Each of these learning processes contributes to
21 the overall learning that takes place in visuomotor adaptation tasks, and although the learning
22 processes and error signals are independent, they interact in a complex manner. We outline many
23 task contexts where the operation of these processes is counter-intuitive and offer general guidelines
24 for their control, measurement and interpretation. We believe this new framework unifies several
25 disparate threads of research in sensorimotor adaptation that often seem in conflict. We conclude by
26 explaining how this more nuanced understanding of errors and learning processes could lend itself to
27 the analysis of other types of sensorimotor adaptation, of motor skill learning, of the neural processing
28 underlying sensorimotor adaptation in humans, of animal models and of brain computer interfaces.

29

30 **Introduction**

31 The experimental study of sensorimotor adaptation has a history that predates the establishment of
32 neuroscience and psychology as formal fields of study (von Helmholtz 1865), yet neither its
33 psychological processes nor neural circuit mechanisms are fully understood. Some blame for this lies
34 in the historical lack of agreement on the exact definition of adaptation and its constituent parts
35 (Franklin and Wolpert 2011; Haith and Krakauer 2013; Held and Freedman 1963; Kornheiser 1976;
36 Redding et al. 2005; Shadmehr et al. 2010; Shadmehr and Krakauer 2008; Wolpert et al. 2011). Here
37 we broadly define sensorimotor adaptation as what takes place when a well-learned skill is modified
38 to fit new conditions, such as when a carpenter borrows a hammer that is a different size than his own
39 (James 1891). This review focuses on a narrower definition of adaptation as a motor learning process
40 that alters future behavior in response to a discrepancy between actual sensory feedback and the
41 sensory feedback that was expected to occur because of the motor command. When our carpenter
42 uses the borrowed hammer, its different dynamics mean that his usual swing will result in unexpected
43 tactile feedback in his hand, along with different visual feedback and potentially a different ultimate

44 outcome for his intended goal. The motor system will automatically adjust itself in this case, tweaking
45 the existing skill until the expected relationship between movements and feedback is re-established,
46 usually reinstating adequate performance.

47 Adaptation is often studied in the laboratory through perturbation of limb motion during a movement,
48 or by perturbation of the sensory feedback caused by the movement. There are many different
49 examples of adaptation tasks, such as saccades and smooth pursuit (Gonshor and Jones 1976;
50 McLaughlin and Webster 1967; Optican et al. 1985), disruption of walking gait (Dietz et al. 1994;
51 Forssberg et al. 1980; Thelen et al. 1987), or reaching with external forces applied to the arm (Bock
52 1993; Fisk et al. 1993; Lackner and DiZio 1994; Sainburg et al. 1999; Shadmehr and Mussa-Ivaldi 1994).
53 This review's primary focus is visuomotor adaptation of manual reaching, as recent experiments have
54 revealed much about the nature of this learning process. Visuomotor adaptation was originally
55 induced by having participants view their arm through displacing prisms (Held and Hein 1958; von
56 Helmholtz 1865), but can also be induced with completely artificial visual feedback mediated by an
57 oscilloscope (Held et al. 1966), and more recently with computer monitors (Cunningham and Vardi
58 1990) or immersive virtual reality headsets (Anglin et al. 2017). We focus on visuomotor adaptation
59 with the expectation that many insights gleaned from our analysis of this form of adaptation will
60 generalize to other subtypes of sensorimotor adaptation and motor skill learning.

61 Historically, many adaptation studies focused on the locus of learning, specifically whether it was the
62 senses, the motor commands, or the connection between these two domains that changed (Efstathiou
63 et al. 1967; Welch 1969). This early work showed that vision, proprioception, and the relationship
64 between the body and extrinsic space can all be altered in response to perturbed visual feedback.
65 However, whenever visual feedback is perturbed, there is always a corresponding change in behavior
66 that cannot be attributed to a retuning of the senses, meaning that its locus must lie either in the
67 mapping between the senses and motor commands, or directly in the alteration of motor commands
68 (see Kornheiser 1976; Redding et al. 2005 for thorough reviews of this topic). This "central" change to
69 the visuomotor mapping is the specific focus of our review of visuomotor adaptation. Several studies
70 suggest that this adaptation alters the displacement vector computed from the difference in the hand
71 and target locations in extrinsic space, specifically altering the movement vector endpoint (Krakauer
72 et al. 2000; Wang and Sainburg 2005; Wu and Smith 2013). Visuomotor adaptation can therefore be
73 seen to primarily alter the step of the motor control hierarchy that transforms movement vectors
74 computed in extrinsic space into intrinsic joint space coordinates, rather than the motor system as a
75 whole (specifically, visuomotor adaptation does not alter of the mapping between joint angle changes
76 and the muscle activation required to change joint angles).

77 This consensus around what was primarily altered in adaptation inspired models of motor learning
78 which assume that adaptation occurred via the modification of an internal inverse model (Atkeson
79 1989; Gomi and Kawato 1992; Hadjiosif et al. 2021; Raibert 1978; Shadmehr and Krakauer 2008). An
80 internal inverse model takes the current state and a desired sensory state, or trajectory of states, as
81 input and outputs motor commands. Many current models have a slightly different framework,
82 positing that motor commands are generated using optimal feedback control, where motor
83 commands are generated by a control policy that minimizes a loss function composed of the explicit
84 desired sensory state and other factors like metabolic cost, pain and reward (Crevecoeur et al. 2014;
85 Diedrichsen et al. 2009; Friston 2011; Kim et al. 2021; Pruszynski and Scott 2012; Scott 2004; Shadmehr
86 and Krakauer 2008; Todorov 2004; Todorov and Jordan 2002; Wong et al. 2015). In this framework,
87 some researchers suggested that adaptation occurs via the adaptation of the internal forward model
88 (Crevecoeur et al. 2020a, 2020b; Izawa et al. 2008). An internal forward model takes the generated
89 motor commands as input and outputs the predicted sensory consequences of the movement. This

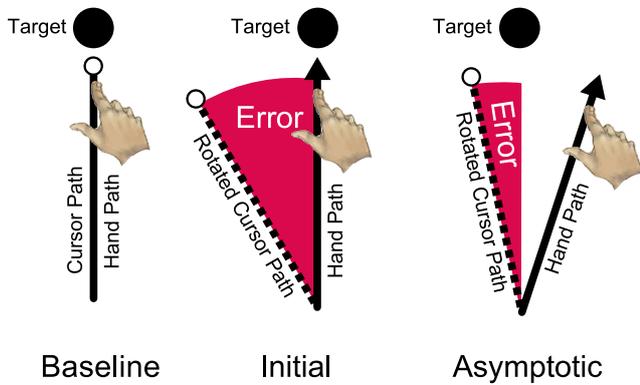
90 internal forward model is taken into account by the control policy during planning. In the optimal
91 feedback control framework, adaptation of the internal forward model leads directly to a change in
92 generated motor commands because it modifies the state estimate (Diedrichsen et al. 2009).
93 Notwithstanding these subtle differences between frameworks, a consensus view is that implicit
94 sensorimotor adaptation (specifically the adaptation of the internal inverse and/or forward models)
95 alters the outputs of the control policy.

96 It is important to disambiguate the above learning, which represents implicit adaptation, from the use
97 of an explicit strategy to compensate for imposed perturbations. A cognitive strategy can encompass
98 many things. In this context we are referring to the explicit decision to re-aim, or change the spatial
99 goal of a reach, so that the participant intentionally plans to move their hand to a location that is
100 distinct from the location of the target. Disambiguation between explicit and implicit adaptation
101 requires specific experimental procedures (Hadjiosif and Krakauer 2020; Maresch et al. 2020a), as the
102 two types of learning result in the same behavior: a single reach that has been adapted to move 15°
103 off midline is kinematically identical to an un-adapted reach that is aimed 15° off midline. Although
104 people tend to fixate the location where they are aiming, this is not necessary (de Brouwer et al. 2018;
105 Rand and Rentsch 2015), meaning that there is not necessarily an external behavioral marker of
106 implicitly or explicitly adapted movements. Similarly, in other movement contexts, the aiming point
107 and the target are not always identical. For instance, while preparing to fire a single arrow, an archer
108 may notice that the wind is blowing to the left and deliberately decide to aim her shot to the right of
109 the bull's eye to compensate. Such a strategy does not reflect a change in the control policy, and it
110 would be inappropriate to characterize it as implicit adaptation to the wind.

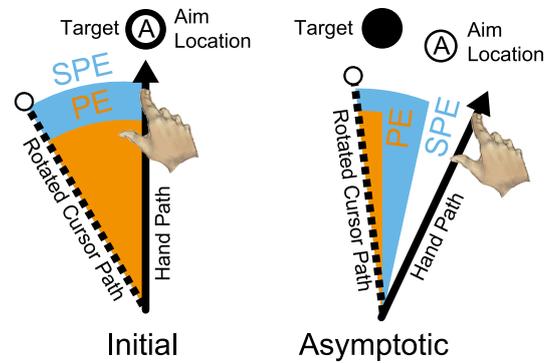
111 We give these examples to demonstrate that the use of an explicit aiming strategy and implicit
112 adaptation could lead to the same change in measured behavior, despite vastly different underlying
113 mechanisms in terms of the motor control hierarchy, neural loci and computational processes
114 (McDougle et al. 2016). In early work, a minority of researchers sought to dissociate the explicit and
115 implicit components of visuomotor adaptation (Weiner et al. 1983; Welch 1969). Today measuring or
116 experimentally controlling the use of strategies during adaptation tasks is becoming a standard in the
117 field (Butcher et al. 2017; Haith et al. 2015; Hegele and Heuer 2010; Heuer et al. 2011; Heuer and
118 Hegele 2011, 2014; Leow et al. 2017, 2018, 2020; Mazzoni and Krakauer 2006; McDougle et al. 2015,
119 2017; Miyamoto et al. 2020; Morehead et al. 2015, 2017; Rand and Heuer 2020; Ruttle et al. 2020;
120 Schween and Hegele 2017, 2017; Taylor et al. 2014; Tsay et al. 2020b; Vandevoorde and Orban de
121 Xivry 2019, 2020a). It is also increasingly recognized that there is a graded boundary between implicit
122 and explicit behavior, which can complicate the differentiation these processes (Hadjiosif and
123 Krakauer 2020; Maresch et al. 2020a).

124 This focus on the implicit/explicit dichotomy led to the observation that these processes may be driven
125 by distinct error signals (Shadmehr et al. 2010; Taylor et al. 2014), with sensory prediction-error and
126 performance error being of particular interest (see below for a definition of these terms, Jordan and
127 Rumelhart 1992). Indeed, recent experiments designed to measure behavioral responses to distinct
128 errors have revealed that there are likely more than two distinct learning processes contributing to
129 visuomotor adaptation. Our primary purpose here is to review this disparate experimental work to
130 describe a coherent and holistic view of reliable data about how visuomotor adaptation occurs in the
131 natural world. Moreover, we believe such a framework will be useful for a diverse group of scientists
132 in the design and interpretation of motor learning and skill acquisition experiments, for both behavior
133 and neurophysiological measures.

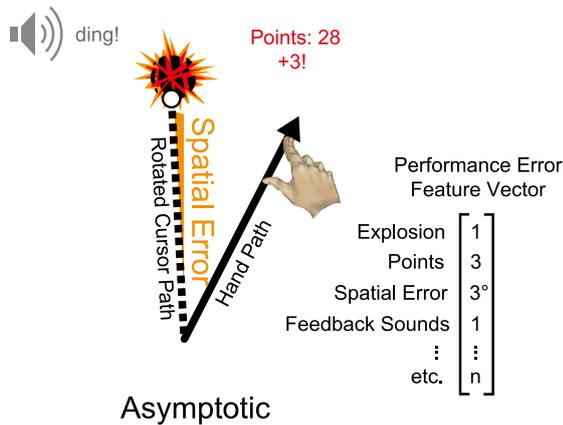
a Traditional Visuomotor Rotation



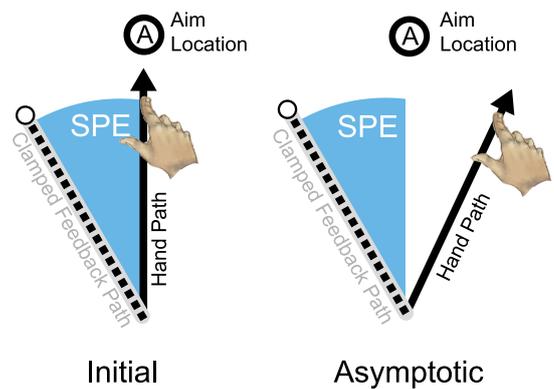
b Errors Revealed by Explicit Aiming Strategies



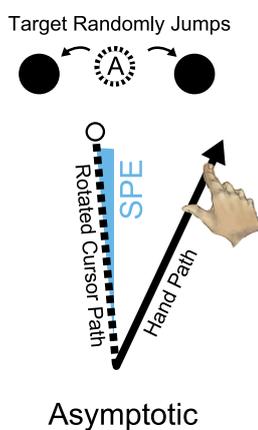
c Performance Error (PE)



d Sensory Prediction Error (SPE)



e Enforced Target Error



f Target Hitting Error (THE)

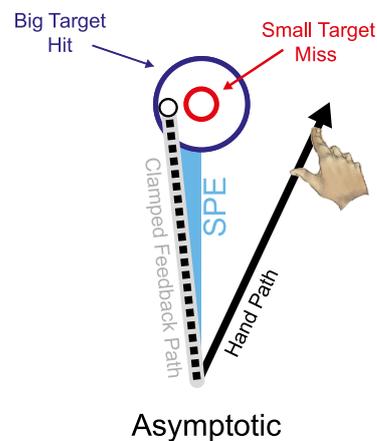


Figure 1 Errors in Visuomotor Adaptation Task Contexts. A) A traditional visuomotor rotation task. The hand of the participant, hidden from view, moves from a start position to the target (black circle). During baseline, the feedback cursor (white circle), shows the actual location of the hand. When feedback is perturbed, the position of the cursor is rotated around the start position, so that it moves in a different direction from the hand when a movement is made away from the center. Later in learning, the participant has altered the direction of movement to counteract the rotation of feedback, bringing the cursor closer to the target (asymptotic learning). The difference between the cursor and target angle (in pink), is the error signal driving learning in most models of motor learning. We refer to this error as the composite error. B) The change in movement direction that counteracts the cursor rotation can be made implicitly or explicitly. Experiments that measure or control explicit aiming strategies reveal that these two types of correction are driven by at least two error signals: explicit strategies by performance error and implicit adaptation by sensory prediction-error. The aiming direction is represented by the A symbol within a circle on the right panel. The task performance error (in orange) is the difference in angle between the target and the cursor. The sensory prediction-error (cyan) is the difference between the aiming direction and the direction of the cursor. C) Performance error in visuomotor adaptation is more than a visuospatial error vector between the cursor and target. On a hit it may include any signal that conveys information about task success, including a visual “explosion” of the target, a pleasant sound and/or numerical points provided after the movement. For a miss, the target may not explode, the sound may be unpleasant and/or points could be withheld or subtracted. These signals of success may accompany or take the place of visual feedback of position. Performance error may best be thought of as a feature vector made up of many disparate elements from sensory and cognitive modalities. D) Sensory prediction-errors are ostensibly generated when sensory feedback is compared to that predicted from the motor command by a forward model. Here we show a visual signal that is thought to generate such an error, isolated from performance errors with the task-irrelevant clamped feedback method. Here the cursor always moves at a fixed angle that is offset from the target, and participants are informed that they cannot control the direction of this feedback. Moreover, they are instructed not to try to control the feedback and to instead ignore it while always moving their unseen hand directly to the target. This manipulation induces implicit adaptation without any changes in aim or performance error throughout the task. Notably, because the clamped feedback angle is fixed and aim is always at the target, the putative sensory prediction-error also remains unchanged throughout the task. E) Another way to isolate adaptation to a sensory prediction-error is to randomly change the sign of performance error on every trial by jumping the reach target out of the way during the second half of movement. This allows trial-to-trial measurement of the same implicit adaptation as task-irrelevant clamped feedback without giving participants information on the nature of the perturbation or providing specific strategies to ignore or aim to a location. There should be no net change in aim in this task over the course of a learning block or within a group of participants as the sign of the jumps is random. The target can also be jumped directly into the path of the cursor so that the movement is always successful. F) The angular deviation of the feedback is fixed with the task-irrelevant feedback method, and at small offsets this may intersect the target if it is large (blue circle, Big target hit) or miss the target when it is small (red circle, small target miss). Along with the target jumping method on the left, this method revealed that there is a third signal, a seemingly binary target hitting error, that modulates implicit adaptation even when it is irrelevant to task performance.

135 Visuomotor adaptation is driven by different error signals

136 Many visuomotor adaptation studies are performed in the center-out reach paradigm (Georgopoulos
137 et al. 1981). This type of task features planar reaches made from a central start position to targets
138 arranged in a circle around the starting point (Fig. 1a, baseline). Visual feedback of their hand position
139 is represented via a cursor on the screen, while direct vision of the hand is typically occluded. In these
140 tasks, people are asked to either to bring their hand to rest within the target or to pass their hand
141 through the target without stopping. Bringing the hand to rest within the target location typically takes
142 more time, and success in this type of reach often requires online correction of the movement.
143 Movements where the hand briefly passes through the target can be made quickly enough (150-
144 200ms) to ensure that online feedback corrections from sensory feedback are minimized or precluded
145 entirely (Elliott et al. 2010; Saunders and Knill 2003). Visual feedback of the hand position is typically
146 presented to provide information on the accuracy of a participant’s movements, either online during
147 the reach or at designated points during the movement, such as the endpoint. This visuospatial
148 feedback of hand position is often supplemented with additional information on movement duration
149 and spatial accuracy via auditory tones, text displays, or changes in the color of objects on the display.

150 Composite error (CE)

151 In the visuomotor rotation task (Fig. 1A, initial and asymptotic), feedback is perturbed by applying a
152 rotation to the position of the hand feedback cursor relative to the start position. This only alters the
153 angle of the feedback, independent of the radial position, meaning the magnitude and speed of the
154 feedback remains unaltered and statistically independent of the perturbation (Krakauer et al. 2000;
155 Pine et al. 1996). Such rotation introduces an error (Fig. 1A), or a difference between what the
156 participant planned to do and what occurred. This error may result in a failure to hit the target entirely,

157 or the task may require the error to be corrected online during the trial. In either case, the imposed
158 error drives adaptation of the reach behavior on subsequent trials, which decays once the
159 perturbation is removed (Tseng et al. 2007). Although the discrepant visual feedback was the only
160 error introduced directly, this usually causes a cascade of other errors. For instance, if the visual
161 feedback cursor did not reach the target in time, the trial may be considered less rewarding by either
162 the participant or the experimental software (registered via sounds for failure, a lack of points
163 awarded, etc.). Internal to the participant, the moment to moment sensory feedback that is predicted
164 for each movement by a forward model will be discrepant. Taken together, these error signals form a
165 composite error that drives adaptation of reaching behavior. This composite error is used by almost
166 all models of motor adaptation until now, as most experimenters did not have a way to differentiate
167 between error types. Recent research has shown that this error can be broken down into constituent
168 parts, and that these unique facets of error drive different learning processes that cause changes in
169 behavior during adaptation tasks. Below, we detail the different constituent error signals that have
170 been identified from the composite error that is introduced by visuomotor perturbations.

171 Performance Error (PE)

172 Performance error is a term for any feedback that conveys information about success in any
173 undertaking. We want to emphasize that performance error is specific to each task and task
174 environment. In natural settings, the task is determined entirely by the organism, as the animal defines
175 its own goals via instinct or reason and finds sensory feedback that is predictive of success (Skinner
176 1981; Tinbergen 1951). In the laboratory, the task is often arbitrary, with the experimenter relating an
177 understanding of the task and what constitutes success via verbal instruction, imitation, and
178 interactive feedback from the task itself. Participants further refine their understanding of the task
179 and its signals for performance error through practice and questions of the experimenter.

180 In a reach adaptation context, the primary performance error metric is the difference between the
181 visuospatial feedback of target position and the hand (Fig. 1C, spatial error). This feedback can be
182 given during or after a movement is complete and may reflect the entire movement or only specific
183 points in the movement. All of these constitute a graded, or scalar, form of feedback that could be
184 reported in one, two or three dimensions. Importantly, some of the visuospatial feedback may be
185 superfluous to the participant's task (e.g. "hit the target"), or all of it could be important (e.g. "move
186 straight and hit the target"). Additionally, a very common task success metric is movement time, which
187 may be reported to the participant numerically, graphically (a number line or bar graph), or with visual
188 or auditory categorical metrics ("too slow", "too fast"). Depending on the task, this space and time
189 feedback may be supplemented by categorical or graded feedback such as pleasant or aversive
190 sounds, "explosions" of the target, points that increment or decrease, money that is earned or lost
191 (Fig. 1C), and primary rewards such as juice or food (in the case of animal experiments). These signals
192 are all sources of performance error. Therefore, performance error should be thought of as a
193 multidimensional error signal gathering all the relevant aspects of the task performance. Put
194 differently, performance error can be thought of as a feature vector of the many factors that may
195 themselves be scalar, categorical, or binary (Fig. 1C).

196 Participants can use performance error feedback, however coarse, to reinstate good performance in
197 response to a perturbation (Butcher et al. 2017; Nikooyan and Ahmed 2015). Such learning can take
198 place gradually or in abrupt steps, and can appear exponential—especially if averaged across
199 participants (Gallistel et al. 2004). The evidence suggests that learning from performance error does
200 not recalibrate internal models, instead it arises primarily from alterations in explicit aiming strategies
201 (van Beers 2009; Wong et al. 2019). This observation is controversial, as it is a long-held view that
202 adaptation occurs in response to performance error (Atkeson 1989; Jordan and Rumelhart 1992). This

203 view was tenable because most studies unknowingly measured a composite of several error types
204 rather than performance error in isolation.

205 Relevant to performance error is the difference between experienced and predicted reward is known
206 as reward prediction-error (Montague et al. 1996). Critically, this is not a primary signal in the
207 environment, but a signal calculated internally by an organism (or simulated by a model). This
208 expectation of reward can be conditioned either passively or actively through classical or instrumental
209 conditioning, respectively. Generation of this error signal is useful for maintaining a well-calibrated
210 valuation of states, stimuli, actions and outcomes (Schultz 2016). It can therefore be seen to indirectly
211 affect learning in adaptation tasks as a variable intrinsic to non-motor decision making. We assume
212 that reward prediction-error is being calculated relative to both graded and punctate performance
213 errors (including primary rewards and punishments, when present) that are experienced on each trial
214 (Fig. 1F). We therefore do not discuss it in further detail, other than to point out that it is intrinsically
215 involved in an organism's internal assessment of its own performance and economic utility in general.

216 Sensory Prediction-Error (SPE)

217 There is good agreement that the motor system feeds corollary discharge of the descending motor
218 commands to an internal forward model so that the future state of limbs can be estimated during
219 movement (Franklin and Wolpert 2011; Shadmehr et al. 2010; Shadmehr and Krakauer 2008; Wolpert
220 et al. 2011; Wolpert and Kawato 1998; Wolpert and Miall 1996; Wong and Shelhamer 2010). It is
221 hypothesized that this sensory prediction is compared to the actual sensory feedback to form the
222 sensory prediction-error, which has long been thought to play a role in adaptation (Jordan and
223 Rumelhart 1992). Importantly, sensory predictions and sensory prediction-errors are generated
224 internally by the organism and can only be indirectly measured or manipulated, barring direct
225 stimulation or recording of neurons in the circuit (Pasalar et al. 2006; Requarth and Sawtell 2014). In
226 visuomotor adaptation experiments, the perturbation of sensory feedback ostensibly induces a
227 sensory prediction-error (Fig. 1D), which results from the difference between the sensory feedback
228 predicted from the motor command (here, a spatially and temporally specific motion of a visual
229 cursor) and the actual sensory feedback (motion of the feedback cursor). In Figure 1D, we show this
230 putative sensory prediction-error in the context of the task-irrelevant clamped feedback task, where
231 participants are informed that the cursor will travel along a specific pre-determined path that is
232 angularly offset from the target and, importantly, that this feedback does not show the position of
233 their hand. Moreover, participants are told that their task is to ignore this motion stimulus and move
234 their unseen hand directly to the location of the target. Despite instructions to ignore this feedback,
235 and an explicit understanding that this feedback is not related to their performance in the task,
236 participants show a robust implicit adaptation that is indistinguishable from implicit adaptation
237 observed in response to conventional visuomotor rotations (Avraham et al. 2021; Kim et al. 2018,
238 2019; Morehead et al. 2017; Poh et al. 2021; Tsay et al. 2020b, 2020c, 2020a, 2021; Vandevorde and
239 Orban de Xivry 2019, 2020b). In these other tasks, rotated feedback has been shown to drive implicit
240 adaptation independent of performance error (Kim et al. 2018; Leow et al. 2018; Mazzoni and
241 Krakauer 2006; Miyamoto et al. 2020; Morehead et al. 2017; Taylor and Ivry 2011; Vandevorde and
242 Orban de Xivry 2019; Wolpert et al. 1995). For both task-irrelevant clamped feedback and relevant
243 perturbed feedback, this adaptation presumably occurs because it induces a sensory prediction-error.

244 In classical visuomotor rotations, sensory prediction-errors and performance errors are conflated the
245 early stage of adaptation, where the perturbed feedback should be considered as a composite error
246 signal (initial adaptation in Fig. 1A). If the participant changes their aim from the visual target's
247 location, their performance error and sensory prediction-error signals will differ from this point in the
248 adaptation period. It is therefore easier to dissociate these errors in tasks where explicit aim is

249 measured (Fig. 1B). Here performance error is represented by the difference between the direction of
250 the cursor's motion and the target angle. Sensory prediction-error, on the other hand, corresponds to
251 the difference between the angle of aim and the visual feedback's direction of motion. It should be
252 noted that sensory prediction-error is a hypothesized signal has not been directly observed in
253 sensorimotor adaptation experiments despite strong theoretical foundations.

254 Target Hitting Error (THE)

255 Target hitting error is a binary error signal that modulates behavior irrespective of the explicit task
256 context. We introduce this term because two independent studies have shown that vision of a cursor
257 intersecting the target of a reach attenuates implicit visuomotor adaptation (Kim et al. 2019; Leow et
258 al. 2018). In one of these studies (Fig. 1D), during the adaptation to a visuomotor rotation, the target
259 of the reach jumped into or away from the path of the cursor. In both types of target jump, the typical
260 relationship between behavior and performance error was eliminated, as the participant was either
261 always successful or unsuccessful. Despite this decoupling of performance error, the authors observed
262 that the adaptation was larger when the target jumped away from the cursor path than when it
263 jumped into the cursor path (Leow et al. 2018). In the other study (Fig. 1E), the researchers used the
264 task irrelevant clamped feedback protocol described above (Fig. 1C) but varied the width of the target
265 (Kim et al. 2019). In the hit condition, the target was large, and the cursor reached the target, while in
266 the miss condition the target was smaller and the cursor always missed the target. Here again,
267 adaptation was larger in the miss condition than in the hit condition. In both sets of experiments, the
268 participants had no control over whether the cursor hit the target, and in one case were explicitly told
269 not to attempt to control this element of the task. Nonetheless, in both cases the task-irrelevant
270 motion of the cursor through the target attenuated the amount of implicit adaptation. It should be
271 noted that both studies showed evidence for a binary, or categorical, target hitting error; there is no
272 published evidence that this signal varies parametrically with the distance of the center of the cursor
273 and target.

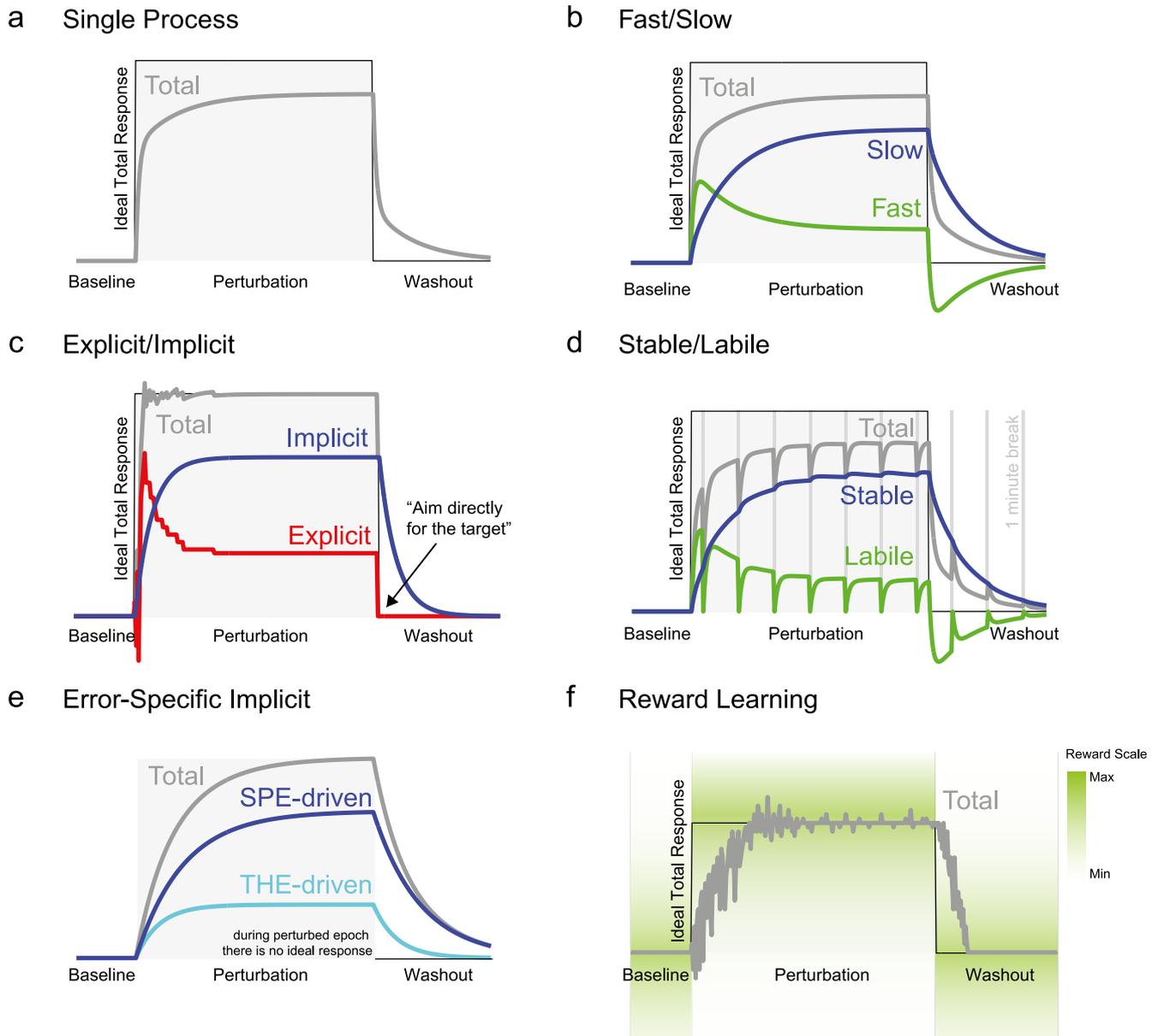


Figure 2 Time course of distinct processes hypothesized to underlie visuomotor adaptation. **A)** Single process. When a visuomotor rotation is introduced at the end of baseline, the motor system adapts the direction of the hand's motion (grey curve) towards the ideal total adaptive response (black trace), which is the opposite of the feedback rotation angle. This change in hand direction over the course of trials represents the total adaptive response. Upon removal of the perturbation (washout period), the adaptation response returns gradually to baseline levels. **B)** Fast and slow processes. The total adaptation response can be decomposed into a fast process that learns fast but forgets rapidly (green curve) and a slow process that evolves slowly but has good retention properties (blue curve). During washout the fast process takes negative values in order to bring the total adaptation curve to baseline levels as fast as possible. **C)** Explicit and implicit processes. The total adaptive response can be decomposed into an explicit and an implicit process (red and blue curves, respectively). At the start of the perturbation period, the explicit process is extremely variable and can take positive and negative values as the participant experiments with different strategies to cope with the perturbation. In contrast, the implicit process evolves more slowly and monotonically. During the washout, participants are instructed to aim their movement directly to the target (often without feedback) so that the implicit process can be measured directly. The implicit curve during the rotation is not measured, but estimated by subtracting reported aim from the measured reach direction. **C)** Labile and stable processes. The processes underlying motor adaptation can be defined as a function of their resistance to the passage of time. In this case, interspersing 1-minute breaks throughout the experiment allows one to look at the effect of time on the adaptation response. Two processes emerge from this manipulation: a stable process whose response does not decay during one-minute breaks and a labile process that decays substantially during these breaks. The labile process appears to learn to both learn and forget faster than the stable process. **E)** Error-specific implicit process. Implicit adaptation to a putative sensory prediction-error differs depending on whether the target was hit by the cursor or not. Specifically, there is less adaptation when the target is hit. Therefore, it has been hypothesized that the implicit adaptation response could be divided into a sensory prediction-error (SPE) driven and a target hitting error (THE) driven process (blue and cyan curves, respectively). **F)** Reward learning process. In the absence of any visuospatial feedback about the participant's performance, the adaptive response can be guided by reward signals such as binary feedback (with gradual perturbation) or with graded feedback (e.g. points, a tone) that varies relative the distance from ideal behavior. In this case, learning is extremely variable but slowly evolves towards the ideal correction for the imposed perturbation.

275 Adaptation consists of distinct processes driven by different errors

276 The dynamics of behavioral changes during sensorimotor adaptation has been interpreted in many
277 different ways, depending largely interests of researchers (Kornheiser 1976; Redding et al. 2005). Here
278 we detail several influential theoretical and task-level descriptions of adaptation, some of which are
279 mutually exclusive. Our later synthesis will seek to explain how the combined behavior of several
280 independent learning processes can explain the behavior observed in each of these contexts.

281 Adaptation to a visuomotor rotation is typically considered as an error learning process where the
282 hand direction on a given movement is determined by a visuomotor mapping from the perceived
283 target direction to a motor command that will move the hand in the same direction. For a movement
284 generated towards a given target direction, the hand's direction of motion depends on the internal
285 state (X_k) of this visuomotor mapping and execution noise (noise).

$$286 \quad H_k = X_k + Noise \quad (Eq.1)$$

287 This visuomotor map is assumed to be at a well-calibrated steady state in the absence of external
288 perturbations, making only small corrections for execution errors. If an external perturbation is
289 introduced, the system will retune its mapping weights, departing from its steady state by a fixed
290 fraction of the error (e) size, parameterized as a learning rate (b). Early models only included the error
291 and learning rate for the state update on every trial (Atkeson et al. 1988; Donchin et al. 2003; Raibert
292 1978; Thoroughman and Shadmehr 2000), but later models introduced a forgetting term (Smith et al.
293 2006). This forgetting factor (a) causes the internal state of adaptation to decay by a fixed percentage
294 between trials. It accounts for two observations, that the adapted memory decays in the absence of
295 feedback (van der Kooij et al. 2015, 2016) and that adaptation is rarely complete, typically leaving an
296 asymptote that is 5% or more short of the imposed perturbation. The following state-space equation
297 illustrates this mechanism. The state of adaptation on the next trial is a function of the amount of
298 adaptation on the previous trials X_{k-1} weighted by a forgetting factor (a) summed with the error
299 observed during the previous movement e_{k-1} weighted by a learning rate (b):

300

$$301 \quad X_k = a \cdot X_{k-1} + b \cdot e_{k-1} \quad (Eq.2)$$

302

303 This simple state-space model describes the dynamics of the adaptation process using the composite
304 error (e_{k-1}) as a signal for learning. Such a model shows a remarkable flexibility, learning to
305 compensate for the perturbations in a large variety of situations (Cheng and Sabes 2006;
306 Thoroughman and Shadmehr 2000) (Fig. 2A). Nonetheless, it suffers from some limitations.

307 Fast-slow learning

308 Single process state-space models cannot account for the double exponential learning curves (initial
309 fast learning period followed by slower learning period) that are commonly observed in adaptation
310 nor can they account for spontaneous recovery of the motor memory and savings. To address these
311 shortcomings, Smith *et al.* (2006) described sensorimotor adaptation as two learning processes
312 operating in parallel: a fast process (x_k^f , red line in Fig. 2B) that learns quickly (b^f) but has poor
313 retention (a^f) and a slow process (x_k^s , blue line in Fig. 2B) that learns slowly ($b^s < b^f$) but has good
314 retention of its state from one trial to the next ($a^s > a^f$).

315

$$\begin{aligned} 316 \quad x_k^f &= a^f \cdot x_{k-1}^f + b^f \cdot e_{k-1} \\ 317 \quad x_k^s &= a^s \cdot x_{k-1}^s + b^s \cdot e_{k-1} \\ 318 \quad H_k &= x_k^f + x_k^s + \text{Noise} \end{aligned} \tag{Eq.3}$$

319 Both processes are driven by the same composite error signal (e_{k-1}), and their learning is summed to
320 affect behaviour with the addition of execution noise (blue line in Fig. 2B), although the processes
321 operate independently. As represented on Fig. 2B, it is interesting to note that the proportional
322 contribution of each process to the total adaptation varies over the course of training. This dual
323 process model can explain double exponential learning curves, and, in limited contexts, the existence
324 of spontaneous recovery and savings of motor memories (Smith et al. 2006; Zarahn et al. 2008). It can
325 be further extended to account for more than two timescales (Kording et al. 2007).

326 Explicit-Implicit learning

327 Sensorimotor adaptation has components that can be categorized based on whether they are
328 accessible by explicit conscious awareness or not. Such distinctions are fundamental for
329 understanding the neurophysiology of memory (Squire 2004). In the context of visuomotor rotation,
330 the explicit process we refer to corresponds to a deliberate and conscious aiming strategy used by a
331 participant to counteract the perturbation (Taylor et al. 2014; Welch 1969). For instance (Fig. 1B), if a
332 cursor deviates towards the left because of a rotation, the participant might explicitly think “aim to
333 the right” of the actual target in order to compensate for the effect of the rotation on her motor
334 performance. This process is explicit because the participant consciously plans to move to a different
335 spatial location than the visual target location. This explicit decision is under volitional control,
336 meaning that the participant may change the location of their aim at will.

337 There are different ways to directly measure explicit aiming in center-out reach tasks. The most
338 straightforward is to have participants report the location of their aim for each reach. Experimenters
339 have had participants report their aim verbally, either by placing landmarks on the screen that
340 participants verbally reference, or by having participants call out imagined numbers on a clock face
341 (Benson et al. 2011; Taylor et al. 2014). For instance, in the study of Taylor and colleagues (2014),
342 numbers were presented on a circle around the starting position. The target corresponded to the
343 number zero. Numbers increased with angular deviation in the clockwise direction and decreased (i.e.
344 became increasingly negative) in the counter-clockwise direction. Before each movement, the
345 participants were required to verbally report the number indicating where they intended their hand
346 to move to (i.e. their “aim”). Aim can also be measured by allowing the participant to position a
347 marker in the workspace with computer peripherals such as a keyboard (Miyamoto et al. 2020), or
348 they can indicate the point of aim by pointing to a touch-screen with their other hand (Bond and Taylor
349 2017). Eye fixation can also be used as a noisy proxy for explicit aim, but it is not a reliable enough to
350 supersede explicit reports (Bromberg et al. 2019; de Brouwer et al. 2018). Moreover, one can employ
351 an aiming strategy at a location that is different from their gaze position (Rand and Rentsch 2015). The
352 difference between these trial-to-trial reports of the intended reach location and the actual reach
353 direction represent implicit adaptation and motor execution noise. When explicit aiming is measured
354 with these techniques, it is typically found that this component of motor learning quickly reaches a
355 high point in the early adaptation period, then slowly decreases to a smaller fixed value. The implicit
356 component evolves more slowly, growing monotonically until it reaches an asymptotic state (Fig. 2C).
357 Several studies have shown that the explicit component is largest during early adaptation to a fixed
358 perturbation, and that it declines but does not entirely go away with extended exposure (McDougle
359 et al. 2015; Morehead et al. 2015; Taylor et al. 2014). Similarly, restricting reaction time has been used

360 to limit the amount of explicit adaptation (Haith et al. 2015; Leow et al. 2017) but this method suffers
361 because explicit strategies can be cached with training and expressed at low preparation times
362 (Huberdeau et al. 2019; McDougle and Taylor 2019). Importantly, this means that reaction time
363 restrictions do not eliminate the use of explicit aiming strategies.

364 Rather than estimating implicit adaptation by subtracting explicit aim from behavior, the accumulated
365 amount of implicit adaptation can be measured directly by giving participants strong instructions on
366 where to aim and withholding feedback at points within a perturbation block or afterwards (Avraham
367 et al. 2020; Hegele and Heuer 2010; Heuer et al. 2011; Heuer and Hegele 2014; Morehead et al. 2015,
368 2017; Taylor et al. 2014; Taylor and Ivry 2011; Vandevorde and Orban de Xivry 2019, 2020a). For
369 instance, in the washout period of Fig. 2C, we illustrate a scenario where participants are instructed
370 to aim directly at the target following a block of perturbation trials. Here, explicit aim is directed to
371 the target location (at 0°) and implicit adaptation causes the hand to deviate from the straight ahead
372 path seen during baseline. While we illustrate this technique for a series of trials on Fig. 2C, this can
373 be also applied for single trials interspersed throughout the adaptation block. In this case, the
374 participants are cued that they should abandon aiming strategies on the next trial. This no feedback
375 catch trial/aftereffect method can be employed in a wide variety of visuomotor adaptation contexts
376 and has the advantage of not providing the participant with a specific strategy. However it has the
377 disadvantage of disrupting the learning process, which introduces a decay of the adapted state, and
378 subsequent learning cannot be considered naïve to externally suggested modifications in aim.

379 The idea that sensorimotor learning has explicit components is not new (Hendrickson and Schroeder
380 1941; Welch 1969). However there has been a great deal of interest in explicit adaptation since it was
381 clearly shown to play a large, persistent, role in sensorimotor adaptation, and that it bears a striking
382 similarity to theorized fast and slow adaptation processes (McDougle et al. 2015). Research on
383 methods for the measurement and control of explicit and implicit learning is progressing rapidly
384 (Hadjiosif and Krakauer 2020; Maresch et al. 2020b), offering many different options that cannot all
385 be detailed here. Care should be taken in navigating this explicit/implicit dichotomy. One thing is clear,
386 there are explicit and implicit learning components of adaptation across all forms of adaptation,
387 independent of the type of perturbation. The measured magnitude of these processes may depend in
388 part on the method used to measure them, and we know the proportion of explicit learning out of the
389 total adaptation differs as a function of the perturbation and the experimental context (Bond and
390 Taylor 2015; Schween et al. 2020). Importantly, throughout this review when we discuss explicit
391 strategies, we are referencing strategies that are consciously and volitionally employed by the
392 participant at the time of their use, not only upon reflection at a later point in time (Hadjiosif and
393 Krakauer 2020).

394 Labile-stable learning

395 Memories for sensorimotor adaptation also vary in their evolution over time. Some show a time-
396 dependent decay within a minute, while others are relatively stable over hours or days. This is not
397 particularly surprising, as it is common to observe that a portion of adaptation decays during breaks
398 when no movements were made (Fig. 2D). The time course of this decay has been systematically
399 investigated over minutes (Alhussein et al. 2019; Hosseini et al. 2017; Joiner et al. 2017; Joiner and
400 Smith 2008; Sing et al. 2009; Zhou et al. 2017). This work suggests a simple dichotomy between the
401 component that decays over time, dubbed temporally labile memory (green line on Fig. 2D), and the
402 component that only decays when movements are made, the temporally stable memory (blue line on
403 Fig. 2D).

404

405 Learning from target “hits”

406 Two studies demonstrated that the intrinsic performance error directly influence the implicit
407 adaptation process (Fig. 2E, Kim et al. 2019; Leow et al. 2018). Here will illustrate this process as
408 observed in the task-irrelevant clamped feedback protocol described above (Fig. 1D) with the use of
409 small and large targets (Fig. 1F). This work showed that the adaptation process did not reach the same
410 plateau in the hit and miss conditions, even though the angular offset of the clamped feedback was
411 identical. When the cursor entirely missed the target, the plateau of adaptation was larger as it
412 resulted in the sum of the implicit adaptation (blue line in Fig. 2E) and of target hitting error process
413 (cyan line in Fig. 2E). In the hit condition, this additional component was absent, and total adaptation
414 remained at the level of the SPE-driven adaptation only. The presence of the intrinsic performance
415 component is thus best demonstrated by contrasting a hit and a miss condition as done in both
416 studies. In both cases, implicit adaptation was modulated by whether the cursor was seen to have hit
417 the target, despite that event’s relevance to explicit performance error.

418

419 Instrumental/Reward learning

420 A variety of studies show that reinforcement learning, or instrumental conditioning, can learn to
421 compensate for a visuomotor perturbations (Butcher et al. 2017; Cashaback et al. 2017, 2019; Codol
422 et al. 2018; Darshan et al. 2014; Holland et al. 2018; Izawa and Shadmehr 2011; Mastrigt et al. 2020;
423 Palidis et al. 2019; Pekny et al. 2015; Therrien et al. 2015). For instance, in such studies, participants
424 are required to reach to a target without visual feedback relating to their hand position during or after
425 their movements. In binary feedback experiments of this type, the only external feedback participants
426 receive is a hit or miss signal (e.g. the target changes color if you hit it). In versions of this task with
427 graded (scalar) feedback, participants may see points or some other non-spatial representation of
428 feedback that indicate the magnitude and/or direction of their reach accuracy relative to the target.
429 To perturb this behavior, the region of the workspace that will trigger the feedback for a target hit is
430 rotated by a fixed angular offset. This requires the participant to change their hand angle in order to
431 receive the same reward feedback that they did under baseline conditions. In graded reward contexts
432 (Fig. 2F), convergence to the new ideal behavior usually progresses on a similar time scale to
433 traditional visuomotor rotations with full online visual feedback. If the feedback is binary, participants
434 do not have any information about the direction of the perturbation and have to find the new reward
435 region purely through exploration, which may result in them not finding the new solution (Manley et
436 al. 2014).

437 This illustrates that any performance error learning problem, such as visuomotor rotation, can in
438 principle be solved by reinforcement learning (Jordan and Rumelhart 1992). Importantly, though these
439 distinct learning algorithms can eventually solve the same problems, there is a mechanistic distinction
440 between the internal process used by unsupervised reinforcement learning and “error-driven”
441 supervised learning processes that are thought to play a major role in implicit sensorimotor
442 adaptation. Such a difference in the nature of the operant process will result in different trial-to-trial
443 behavior during learning. Fundamentally, reinforcement learning algorithms maximize reward by
444 sequentially exploring the action space via random sampling or hypothesis generation, to in turn
445 exploit actions with better outcomes (Dayan and Daw 2008; Marr 1970). Conversely, supervised
446 learning adjusts its actions relative to the error between the teaching signal and feedback from each
447 trial to the next (Marr 1969; Raymond and Medina 2018). In sensorimotor adaptation, the teaching
448 signal for supervised learning is thought to be the sensory prediction-error (Jordan and Rumelhart
449 1992; Shadmehr et al. 2010). The gross learning curves of these processes can appear similar,

450 especially in the presence of execution noise, but their operation is distinct and should be
 451 distinguishable with the right experimental design (Cashaback et al. 2017).

452 There is little doubt that reinforcement learning plays a role in decisions about explicit strategy use in
 453 visuomotor adaptation (McDougle et al. 2016). It is unclear, however, the extent to which extrinsic
 454 reward and punishment affect implicit learning. Reward and punishment have been shown to
 455 modulate learning in adaptation tasks, with differential effects on retention (Cashaback et al. 2017;
 456 Darshan et al. 2014; Gajda et al. 2016; Galea et al. 2015; Izawa et al. 2012; Izawa and Shadmehr 2011;
 457 Nikooyan and Ahmed 2015). It has also been argued that rewards associated with specific actions
 458 bolster retention of motor memories (Galea et al. 2015; Huang et al. 2011; Shmuelof et al. 2012).
 459 However, many of the effects in these studies may arise entirely from explicit strategies (Codol et al.
 460 2018), as studies on adaptation that involve operant learning have often not controlled for this factor.

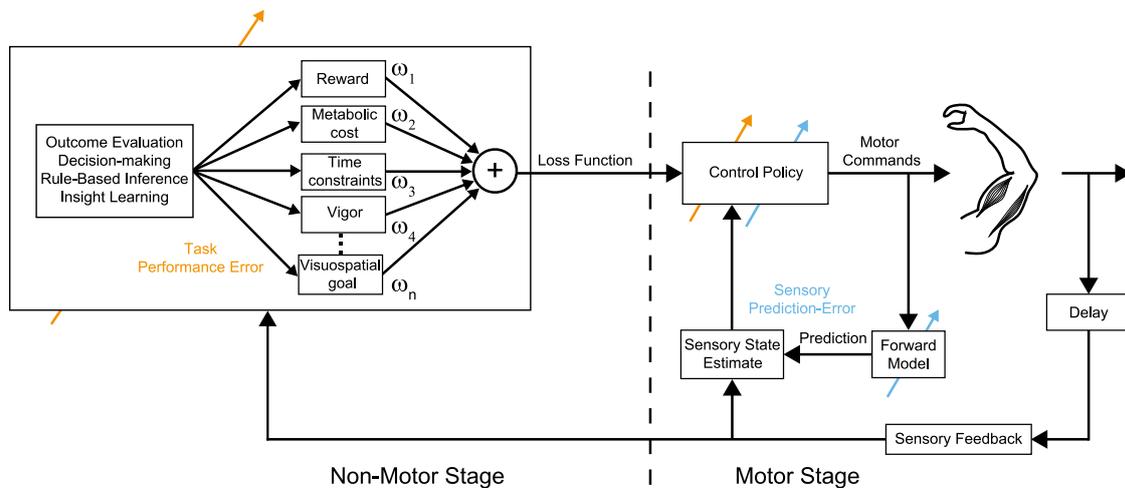


Figure 3 Schematic model for generating goal directed reaching movements and the locus of learning in visuomotor adaptation tasks. The control diagram is composed of non-motor and a motor stages. The motor stage contains all the elements of the conventional motor control scheme: it interacts with the environment via a body that is controlled by motor commands. Noisy sensory information about the state of the body is fed back to the motor system with a delay. This sensory information is integrated with the output of a forward model that uses an efference copy of the motor commands to predict the current and future state of the body. The motor commands are determined by the control policy (sometimes refer to as inverse model), which takes the loss function and the state estimate of the body as input and generates motor commands as an output. Optimal feedback control proposes that the motor commands result from the minimization of the loss function. In our schema, the loss function represents the interface between the motor and non-motor stages. The loss function is shaped by the non-motor part of the system in function of task requirements (instructed speed, accuracy demands, etc.) and internal factors such as motivation or vigor. These factors are not only sensitive to verbal instructions and apparent task conditions but also “high level” cognitive insight. Plasticity in this schematic model is represented by the colored arrows. The task performance error is computed at the level of the non-motor stage based on sensory feedback while the sensory prediction-error is computed in the motor stage based on the output of the forward model and the sensory feedback. We hypothesized that the sensory prediction-error could update both the forward model and control policy. Performance error primarily shapes the loss function but may also directly update the control policy.

461

462 A non-motor stage for the control of visuomotor behavior

463 So far, we have discussed the existence of the numerous processes operating during sensorimotor
 464 adaptation, and the fact that these processes appear to be driven by distinct error signals. Here we
 465 offer a new framework that differs from previous attempts because it distinguishes different types of
 466 errors and articulates which learning processes are driven by these errors. We believe this synthesis
 467 can help explain many counter-intuitive phenomena that have accumulated in the motor learning
 468 literature in recent decades and that it can guide future studies on the neural basis of motor
 469 adaptation. This synthesis is needed because many of the points of view we outlined above were

470 developed to explain the totality of behavior in sensorimotor adaptation, meaning that they are
471 fundamentally at odds. In some cases, this has led to fierce controversies. For instance, the claim that
472 explicit strategies constitute fast learning in sensorimotor adaptation pits multi-rate models (Smith et
473 al. 2006) against explicit/implicit learning (Taylor et al. 2014) but these ideas are not actually mutually
474 exclusive. It is likely that implicit adaptation has processes that learn at different rates, and an explicit
475 strategy can change more rapidly than implicit learning but is also likely to be retained over 24 hours
476 (Wilterson and Taylor 2019). There are also many cases where a failure to consider the different
477 predictions of these frameworks can lead to a general misunderstanding of what behaviors mean in
478 these tasks. We will explore some of these interactions further below.

479 To describe this new framework, we have first updated a traditional sensorimotor control and learning
480 diagram, with the only substantial changes coming at the input stage. Classical control diagrams in the
481 motor learning field start with a “desired” sensory feedback, or sensory goal (Atkeson 1989; Jordan
482 and Rumelhart 1992; Raibert 1978). In previous models, the goal was transformed into motor
483 commands via an internal inverse model (or optimal controller). In the latter case, the motor
484 commands are computed in relation to the loss function, which is not really part of the control scheme
485 (Pruszynski and Scott 2012; Scott 2004; Shadmehr and Krakauer 2008; Todorov 2004; Todorov and
486 Jordan 2002). The loss function not only incorporates spatial constraints throughout the movement,
487 but also many other factors like energy expenditure, movement time restrictions, reward
488 contingencies, and so on (Diedrichsen 2007; Diedrichsen et al. 2009; Harris and Wolpert 1998; Izawa
489 et al. 2008; Nagengast et al. 2010; Scott 2004; Serrancolí et al. 2017; Shadmehr and Krakauer 2008;
490 Todorov and Jordan 2002).

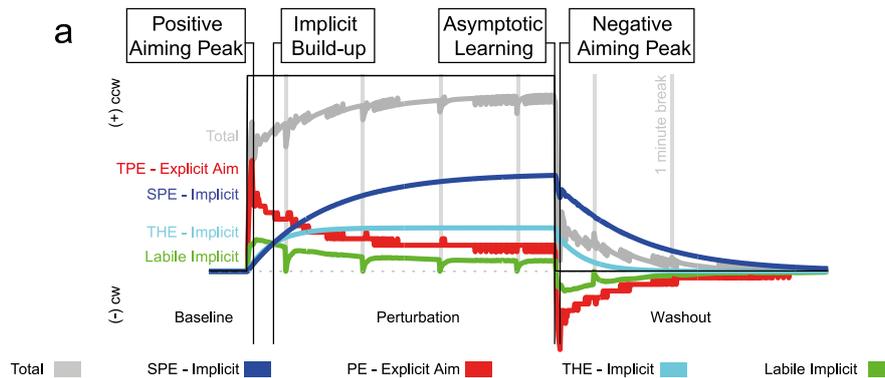
491 While the loss function does not take center stage in most control schemes, here we present it as the
492 interface between a non-motor and a motor stages. Specifically, we propose that the weight of each
493 component of the loss function is determined by cognitive decision-making. Furthermore, we propose
494 that loss function weights in the non-motor stage are adapted as a function of performance error,
495 while the motor stage is directly influenced by the sensory prediction-error. In this framework,
496 learning at the cognitive non-motor stage can alter behaviour without any downstream learning in the
497 motor stage. The weights of the different elements of the loss function are thus specified as a function
498 of cognitive action selection (decision-making) and can be updated on a trial-to-trial basis (Fig. 3) to
499 take into account performance error (van Beers 2009, 2012) or a change in task requirement (Nashed
500 et al. 2012; Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016).

501 We believe the operation of the non-motor stage requires further study in the context of adaptation
502 tasks, but its general operation can be understood from research in other domains. Human decision
503 making is chiefly concerned with explicit goals and rewards, here discussed as elements of a
504 performance error feature vector. Human reasoning is the most flexible and insightful in the animal
505 kingdom, sometimes resulting in abrupt “changes of mind” that emerge from re-evaluation of
506 whether the current movement plan has the potential for success (Pacheco et al. 2020; Sharpe et al.
507 2019; Song and Nakayama 2009). For these changes of mind to occur, the predicted benefit of
508 changing strategies must outweigh the costs in mental effort required to alter the established
509 response contingencies (Kessler et al. 2009; Kiesel et al. 2010; McDougale and Taylor 2019; Monsell
510 2003; Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016; Rogers and Monsell 1995). The idea that
511 changes to the movement strategy rely on executive decision-making mechanisms is further bolstered
512 by work that has consistently linking this learning to working memory capacity (Anguera et al. 2010,
513 2011; Christou et al. 2016; Vandevorde and Orban de Xivry 2020a).

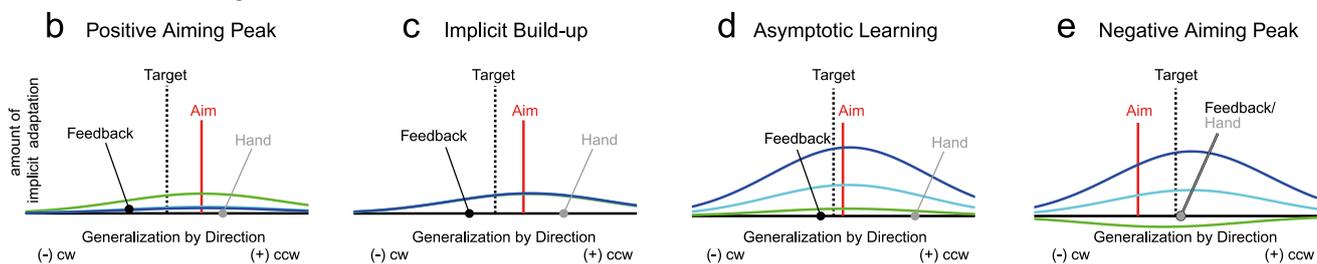
514

515 Once the loss function is specified at the non-motor stage, it is carried over to the motor stage where
516 the control policy then generates a motor command (Fig. 3). As in other frameworks, this motor
517 command is sent to the plant (spinal cord and body) to carry out the movement. A corollary discharge
518 of this efferent motor command is relayed to a forward model (Bridgeman 1995; Sommer and Wurtz
519 2002, 2008), which predicts the future state of the body from the current state and motor command.
520 This future state estimate is useful for many things, but in the context of learning, its sensory
521 prediction is compared to the actual sensory feedback to calculate a sensory prediction-error (Jordan
522 and Rumelhart 1992; Kawato 1999; Wolpert et al. 1995; Wolpert and Miall 1996). This sensory
523 prediction-error influences behavior by adapting internal models (control policy and/or forward
524 model). It is also possible that the performance error might affect the controller directly. We cannot
525 be sure about the locus of implicit adaptation that is driven by target hitting error, given the available
526 data. Although these learning is implicit, we believe it is possible for it to occur within the non-motor
527 or motor stages. Due to a similar lack of data on temporally labile adaptation, we cannot be sure of its
528 locus or even its driving error signal.

Contribution of Learning Processes to Each Trial



Internal Learning State Across Possible Reach Directions



Implicit Modification of Movement on a Given Trial

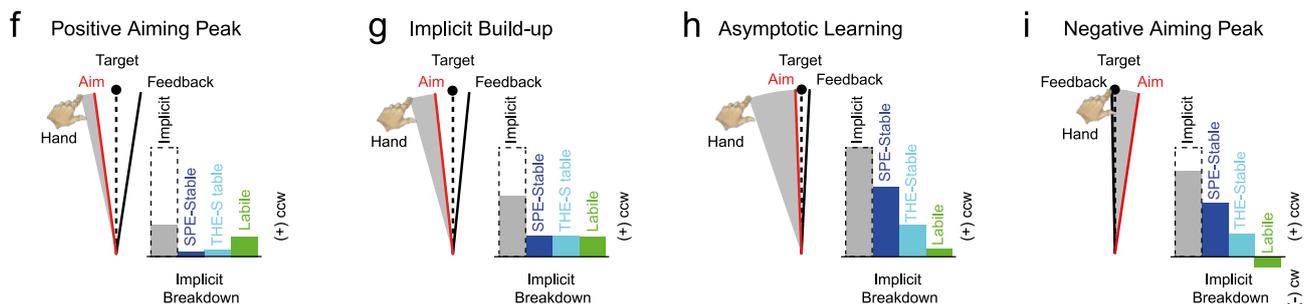


Figure 4 How the processes of visuomotor adaptation contribute to behavior during learning. **A)** Trial-by-trial evolution of the different processes during the adaptation period and washout in the presence of 1-minute breaks (grey vertical lines). Four important time points are highlighted and further described in panels B-I. The positive aiming peak corresponds to the trial where the aiming direction was furthest in counterclockwise direction. Implicit build-up corresponds to a time point early in perturbation block where implicit adaptation is small relative to the adjustment from explicit aim. Asymptotic learning corresponds to the end of the adaptation period where total adaptation is at its maximum. The negative aiming peak corresponds to the moment early in washout where the aiming direction is maximally clockwise. In this simulation, the participant aims in the direction that will lead to best performance throughout the task. Note that the processes sum, although we have shown them each relative to zero. **B-E)** The internal generalization of implicit adaptation (SPE-implicit, THE-implicit and labile implicit) at the four time points highlighted above. The state of each process is represented across different possible movement directions (x-axis) relative to the visual target (vertical black dotted line). This shows the amount of implicit adaptation that is predicted if the participant chose to aim for anywhere other than where they did. These curves show a peak of implicit generalization shifts with the point of explicit aim and that the implicit adaptation that is sampled on a given trial also depends on the explicit aim. Therefore, shifts in aim can cause a substantial change in the expressed amount implicit adaptation (change from D to E). **F-I)** Here, the effect of implicit adaptation (gray wedge) upon a given aimed reach is shown within the task workspace. The bar graphs show a breakdown of the total implicit adaptation (grey bars) into its constituent components (dark blue: SPE-implicit, cyan: THE-implicit, green: labile implicit). Notably, at the negative aiming peak, both the aim and labile learning are opposing the aftereffects caused by the temporally stable implicit adaptation.

530 The many errors and learning processes of visuomotor adaptation

531 Our description of the different errors and processes demands a new description of adaptation that is
532 the sum of a many processes which differ with respect to their driving signal (performance error,
533 sensory prediction-error and target hitting error) and with respect to how they are affected by the
534 passage of time. We propose the existence of four distinct processes, whose contribution to total
535 adaptation will depend on the experimental context.

536 First, the explicit process is driven by performance error (red curve in Fig. 4A). Over the course of
537 adaptation, the contribution of this process increases rapidly, but later decreases until reaching a
538 steady state. Notably, during the washout period (where the perturbation is removed), the explicit
539 process has a negative contribution to the total adaptation. This is because the explicit process takes
540 changes its aim to compensate for the aftereffects of the other processes so that it can maintain good
541 task performance (Yin and Wei 2020). This process is only weakly influenced by the short passage of
542 time—it is a declarative process which should have the same forgetting curve as other declarative
543 memories (Ebbinghaus 1913; Squire 2004). The second process (blue curve on Fig. 4A) is temporally
544 stable implicit adaptation driven by sensory prediction-errors. Third (cyan curve on Fig. 4A) is made
545 up of adaptation that is driven by target hitting error that is stable with respect to the passage of time
546 (Kim et al. 2019; Leow et al. 2018). The last process (green curve on Fig. 4A) is composed of implicit
547 adaptation that decays over a timescale of seconds (Alhussein et al. 2019; Hosseini et al. 2017; Joiner
548 et al. 2017; Joiner and Smith 2008; Sing et al. 2009; Vandevoorde and Orban de Xivry 2019; Zhou et
549 al. 2017). There is not currently any published data bearing on which error drives temporally labile
550 implicit adaptation.

551 These four learning processes we have described sum to affect behavior at any given moment. This
552 causes indirect interactions between them, even though each process otherwise operates
553 independently. For instance, learning from the SPE-driven stable implicit component of adaptation
554 typically causes a decrease in performance error, even though this process is not driven by
555 performance error. In some cases, the same learning process can actually increase performance error
556 (Mazzoni and Krakauer 2006; Miyamoto et al. 2020; Taylor and Ivry 2011). Below, we describe how
557 these processes evolve over the course of an adaptation experiment, and their hypothesized
558 operation of each process in a variety of task contexts. It is our hope that this exercise provides an
559 opportunity design future experiments that account for the operation of the processes we described
560 above.

561

562 Visuomotor Adaptation is the Sum of All Processes

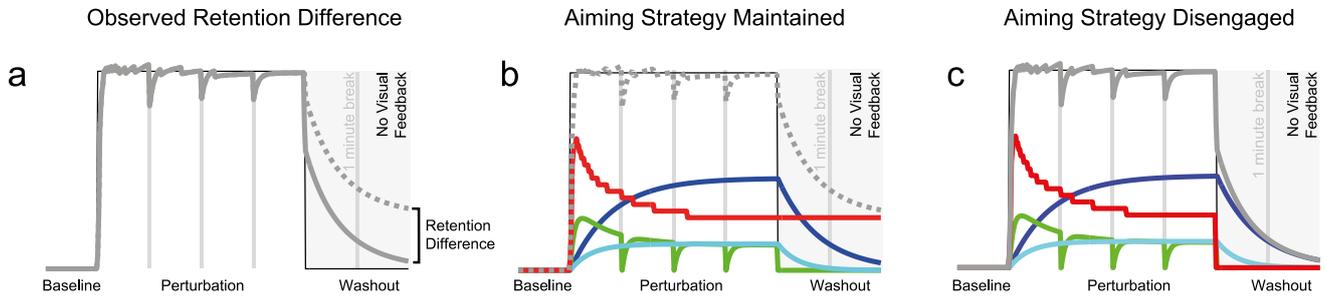
563 In our framework, all the learning processes sum to influence the direction of a given reach. During
564 baseline conditions, and at asymptotic learning, these processes reach a stable and predictable steady
565 state, but their interaction can be complex and difficult to intuit at other points of the learning curve
566 and especially near transitions in the experimental context such as the onset or offset of a
567 perturbation (Fig. 4A). These interactions can be particularly counter-intuitive because implicit
568 adaptation is generalized relative to the angle of aim (Fig 4B-E; Day et al. 2016; McDougale et al. 2017).
569 This means that changes in aim during a visuomotor adaptation task necessarily shift the peak of
570 implicit learning as the point of aim moves in the workspace (Fig. 4B,C). To point, if a participant aims
571 far away from the target, the locus of implicit generalization will be far away from the target (Fig.
572 4B,E). This seemingly should have the biggest effect early in a rotation when aiming is greatest, but
573 implicit adaptation has not yet had time to accumulate so it is of little consequence (Fig. 4B). As implicit

574 adaptation grows, the difference between the peak of generalization at the aim point and implicit
575 adaptation at the target will also increase (Fig. 4C). However, this implicit change in hand position will
576 also cause explicit aiming to decrease so that good task performance is maintained (Taylor & Ivry,
577 2011; Taylor, Krakauer & Ivry, 2014; Miyamoto, Wang & Smith, 2020). This means that the peak of
578 implicit generalization will be closest to the target when learning is asymptotic (Fig. 4D). Whether
579 there will be much difference between the level of implicit learning at the target and at the point of
580 aim depends upon the size of the perturbation, as larger rotations require aiming further from the
581 target, and implicit adaptation is limited in the magnitude of its adjustment (Bond & Taylor, 2015;
582 Morehead *et al.*, 2017; Kim *et al.*, 2017).

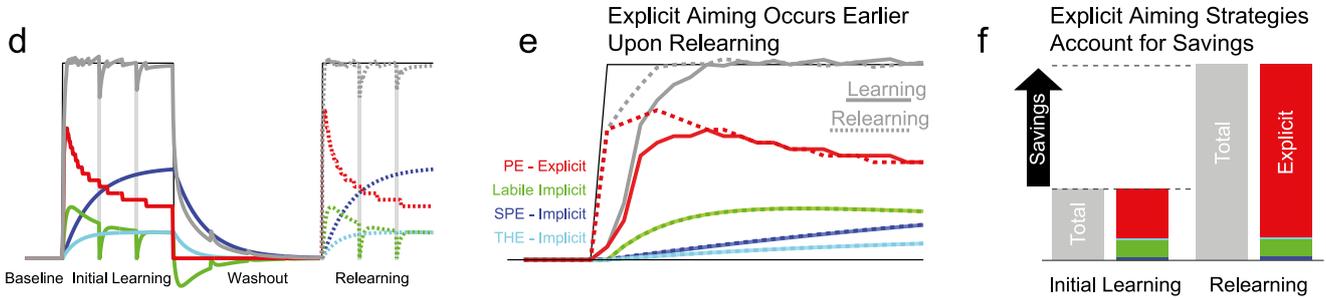
583 The effect of explicit aim on implicit learning levels is greatest when a perturbation is removed, or
584 changes sign. In this case explicit aiming may change drastically (Fig. 4E), which will also cause the
585 expressed level of implicit learning to change, and this may be a pronounced difference (Fig. 4I,
586 negative aiming peak). This hopefully makes clear that aiming in visuomotor adaptation tasks is never
587 “just aiming.” There is an underlying generalization of these processes, and they are related to the
588 point of aim, as illustrated in Figure 4B-E. It is important to measure or control aiming throughout
589 experiments because learning and expression of implicit motor memories are influenced by the
590 explicit aim. The size and sign of these processes can vary depending on the conditions of the
591 experiment, as shown by contrasting the simulated contribution of each process to behavior at specific
592 trials in Figure 4F-I. Given the potential for many different combinations of these processes, it is
593 important to understand how they operate and best to predict their operation with a model.

594

Control or Measurement of Explicit Aim is Critical for Interpreting Aftereffects



Savings is a Function of Explicit Recall of an Aiming Strategy



Error Sensitivity May be Different for Each Learning Process

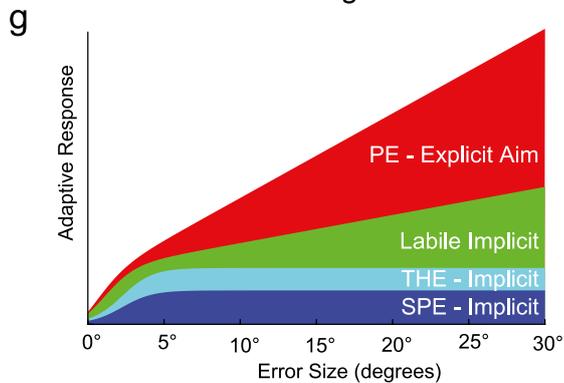


Figure 5 Specific cases where multiple learning processes can be misunderstood. First Row: control or measurement of explicit aim is critical for measuring an implicit aftereffect. A) Effect of instruction on total adaptation measured during a retention period (grey rectangle) in the absence of any visual feedback. The dotted curve illustrates differences in retention that have been observed in many experiments. B and C) illustrate how a simple change in aim can lead to the solid or dotted gray lines observed in A). Importantly, only aim has changed over these two simulations, but they can be misinterpreted as a difference in retention of an implicit motor memory if aim is not measured or controlled. Red, dark blue, cyan and green correspond, respectively, to the explicit, SPE-implicit, THE-implicit and labile implicit processes. SPE: sensory prediction-error; THE: target hitting error. Second Row: Savings upon relearning occurs because explicit aiming strategies are re-engaged during relearning. D) Evolution of the different processes underlying adaptation during learning and relearning. E) Same as D but learning and relearning are superimposed. Solid line: processes during learning; Dotted lines: processes during relearning. G) breakdown of total adaptation into the subprocesses for the first trials of the learning (left) and of the relearning (right) periods. Third Row: Hypothesized response for each component of motor adaptation at different error sizes. The x-axis provides the perturbation size while the y-axis reflects the amount of adaptation. The height of each layer represents the amount of adaptation from each of the processes. The sum of all the layers gives the total adaptation response to a specific error.

595 If aiming is not measured, or experimentally controlled, it can have important consequences for
596 experiments. For instance, if two groups of participants showed similar learning during a perturbation,
597 but aimed to different directions during washout, then the measured after-effects could be quite
598 different (Fig. 5A-C). Whatever the reason for the difference in aiming during washout, a breakdown
599 of these aftereffects into their constituent parts would reveal differences in both explicit and implicit
600 learning processes. Without assessing aim, these aftereffects may be interpreted as implicit motor
601 memories that whose spatial locus is the direction of the target. This is a mistake that has been made
602 frequently with a prevalent experimental design that measures the decay of learning by removing
603 visual feedback (Fig. 5A; Galea et al. 2011, 2015; van der Kooij et al. 2016; Shmuelof et al. 2012; Smeets
604 et al. 2006). Many studies using this design did not disambiguate between implicit motor memories
605 and explicit aiming strategies, complicating the interpretation of their data to the point that they need
606 to be re-examined with these controls in place. To be specific, these studies have interpreted
607 differences in aftereffects during no-feedback conditions as differences in implicit motor memory
608 retention, when the differences are likely a function of aiming.

609 This complication for aftereffect assessment makes it necessary to use clear instructions for strategy
610 use with these experimental designs. In experiments where the removal of the perturbation is cued
611 and participants are instructed to give up any explicit strategies, behavior first shows an initial aim-
612 related drop from instructions, and then subsequent changes in behavior directly correspond to the
613 decay in implicit processes (Avraham et al. 2021; Codol et al. 2018; Hegele and Heuer 2010; Heuer and
614 Hegele 2008; Holland et al. 2018; Taylor et al. 2014). Measurements of aftereffect magnitude and
615 decay are best performed in the absence of feedback, as visual feedback could drive sensory
616 prediction-errors, performance errors, or target hitting errors. In general, it is always a good idea to
617 be cognizant of how errors will drive different learning processes.

618 A similar situation arises in savings designs, where the same perturbation is presented to the
619 participants in two different experimental blocks separated by a period of rest or by a washout block.
620 In this case, savings corresponds to a faster speed of relearning compared to the initial learning.
621 Savings upon relearning has been repeatedly observed in visuomotor adaptation (Krakauer et al.
622 2005), but it is only recently that was this savings attributed to recall of an explicit aiming strategy
623 (Haith et al. 2015; Morehead et al. 2015). In Figure 5E-F, we illustrate how savings arises solely from
624 recall of an explicit strategy, with implicit mechanisms that learn at the same speed both initially and
625 upon relearning. There remains some debate about whether implicit processes also show savings, but
626 the lion's share of the increase in relearning speed clearly arises from non-motor mechanisms and
627 recent work suggests that implicit adaptation is actually attenuated upon relearning (Avraham et al.
628 2021; Huang et al. 2011; Leow et al. 2020; Orban de Xivry and Lefèvre 2015; Yin and Wei 2020).

629 So far, we have discussed block designs, where there is a strong incentive to change strategy when
630 the same perturbation is used in a long set of trials (Morehead et al. 2015; Taylor et al. 2014; Wilterson
631 and Taylor 2019). However, there is not necessarily utility in adjusting for an error when visuomotor
632 perturbations are inconsistent or unpredictable (e.g. zero-mean random perturbation where
633 perturbations of different amplitudes and direction are randomly interspersed among non-perturbed
634 trials). The consistency of the perturbation across trials modulates the overall adaptive response (Fine
635 and Thoroughman 2006, 2007; Gonzalez Castro et al. 2014; Herzfeld et al. 2014; Marko et al. 2012;
636 Scheidt et al. 2001; Vandevorode and Orban de Xivry 2019; Wei and Kording 2009). Decomposing this
637 overall adaptive response into explicit and implicit mechanisms shows that the contribution of an
638 explicit strategy increases with the predictability of the perturbation, while implicit adaptation is
639 mostly invariant to the perturbation context (Avraham et al. 2019; Hutter and Taylor 2018).

640 We believe the operation of the motor and non-motor processes in visuomotor adaptation explain
641 this difference in the response to errors when perturbations are consistent (on balance more likely for
642 a given perturbation to occur) and inconsistent (or unpredictable) contexts. Explicit aiming strategies
643 are chosen in the non-motor stage based on the expected utility of each movement strategy's
644 outcome (Skinner 1981; Trommershäuser et al. 2003, 2008). Therefore, when perturbations are
645 consistent, the use of a strategy to counteract the perturbation will result in less performance error.
646 However, if perturbations of different amplitude and direction are randomly interspersed, then aiming
647 anywhere else will just as likely increase performance error as decrease it (Srimal et al. 2008). In this
648 context it could take as little as a single trial for a participant to abandon an aiming strategy, as it is
649 well established humans are remarkably sensitive the degradation in the contingency between the a
650 particular movement strategy and its outcome (Fellows and Farah 2003; Shanks and Dickinson 1991).

651 This provides some clarity for the longstanding problem of sensitivity to error size in sensorimotor
652 adaptation. Explicit strategies are selectively engaged if they are predicted to have a positive expected
653 utility in terms of performance error (Fig. 5H). When employed, the contribution of the explicit
654 component of adaptation to overall adaptation is roughly linearly proportional to the performance
655 error size. Conversely, temporally stable implicit adaptation is marked by a linear response to error
656 sizes below 5°, and a saturated response of the same size for larger errors (Avraham et al. 2019; Bond
657 and Taylor 2015; Hutter and Taylor 2018; Kim et al. 2018). It is unclear whether temporally labile
658 adaptation can be selectively disengaged in the manner of explicit strategies, but we have
659 hypothesized that it is roughly linearly proportional to the composite error size. This error sensitivity
660 function provides an outline of the trial-to-trial operation of the motor system in response to errors,
661 when coupled with mechanism that will selectively engage explicit strategies depending on their
662 expected utility.

663 Thinking about the motor system's response to visuomotor perturbations as a composite of these
664 processes also informs more complicated task designs, such as that employed by Mazzoni & Krakauer
665 (2006). In this study, the researchers applied a visuomotor rotation of 45° but, after a few trials,
666 informed their participants about the existence of the perturbation, its amplitude and its direction. In
667 addition, a visual marker on the screen cued the aiming strategy that could be used to solve the
668 visuomotor rotation. When instructed to do so, participants were able to bring their invisible hand
669 towards the cued location in order to bring the cursor on the target in a single trial. While this
670 experimental manipulation mostly negated the performance error, the sensory prediction-error was
671 unchanged (the difference between the point of aim and the direction feedback was observed to
672 move). This sensory prediction-error caused implicit adaptation in the direction opposite to the cursor
673 rotation, which caused performance error to increase in opposition to the sensory prediction-error.
674 This is a case where the interaction of explicit and implicit processes can be seen, so that explicit aim
675 is adjusted in response to performance error even when strong instructions to aim at one specific
676 point are provided (Taylor and Ivry 2011). The development of techniques to measure explicit aiming
677 has helped clarify what occurs in this case, so that the overall behavior measured is best described as
678 a dynamic tension of explicit and implicit processes that are driven by different error signals
679 (Miyamoto et al. 2020; Taylor et al. 2014).

680 These examples in the context of aim-dependent generalization, after-effects, savings and error
681 sensitivity demonstrate the importance of measuring the contributions of explicit and implicit
682 processes or of controlling the errors that drive these processes in visuomotor adaptation
683 experiments. It is important to anticipate the operation of these processes, and it ideally models
684 should be used simulate how errors and learning will evolve during any given task.

685 Looking beyond our current framework

686 We introduced a novel synthesis of the learning processes involved in visuomotor adaptation, and the
687 signals that drive their operation. There are many implications of our framework, both proximally for
688 sensorimotor adaptation experiments, and distally for general learning and skill acquisition. The fact
689 that these processes exist and learn from different errors means that researchers must take care when
690 designing experiments in humans. Moreover, this applies to animals where it is common to motivate
691 participants with primary rewards during learning, and much more difficult to measure explicit
692 awareness. Ideally, experiments would be designed so that the operation of each process and its
693 driving signal is known. We believe this would greatly aid both the development of process-level
694 models of sensorimotor adaptation and the understanding of its neurophysiological underpinnings.
695 This approach, of breaking down the driving signals and constituent learning processes, can be
696 generalized to other forms of learning such as sport or skill acquisition with brain-machine interfaces.

697 Beyond visuomotor rotations

698 Our framework was developed from the results of visuomotor rotation experiments. However, we
699 strongly believe that the errors and processes we outlined are operative in other forms of visuomotor
700 adaptation. This includes gains applied to the radial component of a center-out reaches. In gain
701 adaptation, the radial extent of the movement is perturbed by a given scale. For instance, making a
702 10cm point-to-point movement will be visually rendered as making a 12cm movement if the gain is
703 set to 1.2. Humans adapt more quickly to gain adaptation than to visuomotor rotation and tend to
704 generalize this learning globally to all reach directions, whereas learning from visuomotor rotations is
705 generalized as mixture of local and global changes to other reach directions (Brayanov et al. 2012;
706 Krakauer et al. 2000; Pine et al. 1996). Gain adaptation has not been explored in terms of explicit and
707 implicit learning, or any of the other learning processes we have outlined. The learning differences
708 between rotations and gains could come about may be because gain adaptation has a different
709 balance of learning processes, (e.g. much more of an explicit component), or because the underlying
710 mechanisms of implicit learning processes are fundamentally different (e.g. basal ganglia reward-
711 dependent updating of global movement scaling versus sensory prediction-error updates of
712 movement vectors). These possibilities for explicit mechanisms in the context of gain adaptation are
713 so understudied that we cannot say almost nothing about them.

714 Similarly, we expect that our framework extends to prism adaptation, where the presence of multiple
715 learning processes (Kornheiser 1976; Martin et al. 1996; Redding et al. 2005; Weiner et al. 1983; Welch
716 1969) and the importance of performance error and sensory prediction-error (Gaveau et al. 2014)
717 have been acknowledged for a long time. Moreover, explicit aim has been measured throughout the
718 course of prism adaptation (Leukel et al. 2015). We therefore expect that many of the processes we
719 have outlined will play a role in prism adaptation, but it is also likely that there are additional processes
720 that play a prominent role in prism adaptation. For instance, it is more common in prism adaptation
721 for the subjective sense of straight ahead to be recalibrated, along with other senses like
722 proprioception (Harris 1974; Redding et al. 2005). Our framework does not specifically account for
723 recalibration of the senses, or high-level constructs like straight ahead because they are not observed
724 in most contexts. Specifically, if the direction of movements is balanced as in a center-out reach task
725 that span 360°, most of these effects will not occur. We believe it would be worth extending and
726 modifying our framework to build a multiple process description of prism adaptation, although that is
727 outside the scope of the current review.

728 Our framework is also relevant to another classic visuomotor perturbation, mirror-reflected visual
729 feedback (Snoddy 1926; Starch 1910). It has been noted that the eventual learning from such feedback

730 is more akin to *de novo* skill learning than adaptation (Hadjiosif et al. 2020; Lillicrap et al. 2013; Telgen
731 et al. 2014). However, it appears that many, or all, of the processes we outlined in our schema are
732 operative during this learning. Indeed, obligatory implicit adaptation that is driven by sensory
733 prediction-errors may actually be maladaptive in such an environment, and such learning must be
734 overcome with practice (Lillicrap et al. 2013; Wilterson and Taylor 2019). Learning at the level of
735 explicit aiming can only partly explain this compensation, making it likely that the longer-term learning
736 in mirror reversal tasks constitutes a skill learning process that is not outlined in our framework. How
737 skill learning relates to our framework is a pertinent question that we will address further below.

738 [Beyond perturbation of the visual feedback](#)

739 The proposed schema was built upon results obtained in visuomotor rotation experiments, and it is
740 easy to see how it generalizes to other forms of visuomotor learning. However, we believe that the
741 errors and processes that we discuss and synthesize play a role in other forms of sensorimotor
742 adaptation of reaching. These include adaptation observed in response to perturbations that affect
743 intersegmental dynamics of the limb (Bresciani et al. 2002; Krakauer et al. 1999; Lackner and DiZio
744 1994; Sarlegna et al. 2010; Sarwary et al. 2013; Shadmehr and Mussa-Ivaldi 1994). There is good
745 reason to think that neural locus of internal model adaptation for intersegmental dynamics is distinct
746 from visuomotor adaptation, suggesting that there may be fundamental differences between
747 adaptation of dynamics and visuomotor maps (Arce et al. 2010; Donchin et al. 2012; Perich et al. 2018;
748 Rabe et al. 2009), but this does not necessarily mean that the types errors and learning processes that
749 adapt movements are any different.

750 When adaptation of intersegmental dynamics is induced with force-fields, there is a clear contribution
751 of both explicit and implicit learning processes (Hwang et al. 2006; McDougle et al. 2015; Schween et
752 al. 2020). Explicit learning plays a smaller, but still substantial, role in the adaptation of dynamics
753 compared to visuomotor adaptation. It is, however, difficult to compare the magnitude of these force
754 field strategies with visuomotor contexts where the size of the perturbation determines the
755 magnitude of strategy as it is both rare and complicated for force field experiments to compare
756 adaptation to curl fields of different strength. Aside from the explicit/implicit divide, it has been shown
757 that approximately ~20% of the adaptation observed in single target force field studies is temporally
758 labile (Sing et al. 2009). This limited information constitutes the extent of the available knowledge
759 about the different processes and errors involved in adaptation of intersegmental dynamics, making
760 it rather limited in comparison to visuomotor adaptation. We believe that it would be a great boon to
761 understanding of motor learning if future dynamics adaptation tasks were designed to measure
762 learning relative to performance errors, sensory prediction-errors, and the operation of the various
763 implicit and explicit processes that we have outlined in our framework.

764 [Beyond perturbations of the upper limb](#)

765 We expect that our framework should also generalize beyond the arm, to adaptation that occurs with
766 any effector. For instance, in speech adaptation, participants speak words with specific phonemes and
767 their auditory feedback is shifted in phoneme space, so that the auditory outcome is perceived as a
768 different word (Houde and Jordan 1998). This distortion of the audiomotor mapping of speech is
769 analogous to sensorimotor perturbations of the arm, and participants respond by changing their vocal
770 output so that the auditory feedback matches that of their intended target word (Parrell et al. 2019).
771 Performance error here is well-defined (difference between the target and produced sounds), and this
772 performance error could engage explicit components of the speech production, and cognitive
773 strategies similar to those seen in reaching, such as feedback corrections (Kim and Max 2021; Parrell
774 et al. 2017). Similarly, speech adaptation is also sensitive to reward prediction-error (Parrell 2020).

775 Speech adaptation is uniquely interesting because the movements involve control of the tongue, a
776 which is a muscular hydrostat whose control involves no skeletal joint angles (Kier and Smith 1985).

777 In split-belt locomotor adaptation, people are asked to walk on a treadmill while the two belts of the
778 treadmill move at a different speeds. Participants can compensate for this difference in speed by
779 increasing the asymmetry in step frequency or length between the two legs (Dietz et al. 1994; Prokop
780 et al. 1995; Reisman et al. 2005; Torres-Oviedo et al. 2011). Initially, it is common to see both
781 compensatory mechanisms, but over training there tends to be a decrease in step length asymmetry
782 using both spatial (change in the location of the foot landing) and temporal strategies (change in the
783 timing of the foot landing) (Darmohray et al. 2019; Finley et al. 2015; Torres-Oviedo et al. 2011). A
784 distinct, but similar, form of adaptation in step length asymmetry can be induced purely by perturbing
785 visual feedback that corresponds to step length without changing belt speeds (Kim and Krebs 2012).
786 Split-belt locomotor adaptation has been shown to have explicit components (Roemmich et al. 2016),
787 and the gait adaptation induced by visual feedback alone can be attributed entirely explicit to an
788 explicit strategy (French et al. 2018). This research suggests that a schema very similar ours should
789 apply to locomotor adaptation. In the standard gait adaptation task where participants look straight
790 ahead while trying to walk normally, it is difficult to define performance error as this is largely
791 determined by the participant. For both the Roemmich and French studies, the addition of visual
792 feedback for step length and the introduction of a goal state for this feedback helps with quantifying
793 part of the performance error landscape, and it is possible to relate adaptive corrections to this
794 quantity. It is important to note, however, that we should not assume that this artificial task
795 performance feedback replaces more intrinsic elements of the performance error feature vector, such
796 as a sense of stability, biomechanical or cognitive effort. Metabolic factors are likely given a much
797 higher weighting in the loss function of locomotor adaptation, as the costs in walking are an order of
798 magnitude greater than reaching (Finley et al. 2013; Huang et al. 2012; Sánchez et al. 2017). Given this
799 reality, it has been suggested that energy minimization may be the primary driving factor in split-belt
800 adaptation (Finley et al. 2013). Moreover, it is difficult to precisely characterize sensory prediction-
801 errors, which may play a role in the implicit components of split-belt adaptation.

802 Eye movements can also adapt to external perturbations (Fukushima et al. 1996; Lisberger and Kahlon
803 1996; McLaughlin 1967; Paige and Sargent 1991). In saccade adaptation (Herman et al. 2013; Tian et
804 al. 2009), the target that the participants directs his gaze to is displaced during the saccade so that
805 vision of the target is suppressed. The target can be displaced along the primary axis of movement
806 (gain up/down adaptation), or it perpendicular to the direction of movement (cross-axis adaptation).
807 In line with our schema, saccade adaptation is well characterized by more than one learning process
808 that adapt at different speeds (Chen-Harris et al. 2008; Ethier et al. 2008a, 2008b), and saccade
809 adaptation can be driven (perhaps solely) by reward prediction-error as well (Madelain et al. 2011).
810 Though there is a very salient performance error in this task, termed the retinal error, there is evidence
811 that sensory prediction-error is one of the main contributors of saccade adaptation. Namely, if the
812 eye lands between the expected landing position and the target, the sensory prediction-error points
813 in the opposite direction than retinal error, the adaptation will follow the direction of the sensory
814 prediction-error and not the performance error (Wong and Shelhamer 2010). Yet, it is clear that
815 performance error does influence saccade adaptation. For instance, a clever manipulation that took
816 advantage of the execution variability in saccades extinguished the target at the end of the saccade,
817 but only for movements that were smaller than the median execution errors. This led to an increase
818 in saccade amplitude, even though these movements should not have produced a sensory prediction-
819 error (Collins and Wallman 2012). Thus far, studies have been limited to categorical eliminations of
820 performance error or sensory prediction-errors. The parametric contribution of these errors to
821 saccade adaptation have not yet been quantified.

822 Here we have discussed three types of sensorimotor adaptation that are commonly studied in
823 humans, but there are many more. We believe that our general approach, characterizing errors and
824 learning processes, can and should be extended to all these distinct forms of adaptation by experts in
825 those subfields.

826 Beyond motor adaptation

827 Our schema attempts to characterize the errors and learning processes that are involved in
828 adaptation. An unresolved argument in the field of motor learning is whether sensorimotor
829 adaptation is integral to, and representative of, motor skill learning, or whether it is a distinct form of
830 learning that calibrates existing sensorimotor skills. Importantly, much of the theoretical basis of
831 “error-based” learning and internal model theory was created to describe *de novo* learning of a multi-
832 jointed robot arm, to only later be adapted to human motor learning (Atkeson 1989; Cheng and Sabes
833 2006; Jordan and Rumelhart 1992; Raibert 1978; Thoroughman and Shadmehr 2000). Models of
834 sensorimotor adaptation are therefore models of motor skill learning at a fundamental level.
835 Nonetheless, it has been argued that adaptation is a distinct learning process (Krakauer et al. 2019).
836 We feel it is important to acknowledge this controversy, but wish to leave it aside, as we are of a mind
837 that an application of our general approach would greatly aid the study of skill acquisition throughout
838 learning, whether or not it is one in the same as adaptation.

839 Skill learning has long been thought to involve more than one learning processes, and has long
840 theorized that the total measured skill represents the summed output of subskills that are learned in
841 parallel (Snoddy 1926; Starch 1910; Thurstone 1930). Moreover, the observation that skilled
842 performance involves explicit and implicit mechanisms is nothing new (Adams 1987; Hendrickson and
843 Schroeder 1941). Indeed, a primary characterization of skill learning is that performance transitions
844 from an initial declarative process to a non-verbalizable, implicit state (Fitts and Posner 1967). Skill
845 acquisition therefore has many parallels to our sensorimotor adaptation framework. What we believe
846 is missing from this literature is a precise characterization of the signals, or errors, that drive this
847 learning and, for any given skill, a description of the myriad processes that may be driven by these
848 errors. As Thurstone (1930) described, each complex skill is likely composed of a set of subskills that
849 learn at their own rates. To truly understand a complex skill, it is necessary to understand most of the
850 component processes of the skill and what drives them, so that their evolution can be tracked and
851 modelled over the course of learning.

852 Beyond behavior

853 Many studies have attempted to elucidate the neural basis of sensorimotor adaptation. The methods
854 employed are nearly as varied as the field of neuroscience itself, from the study of patients with
855 neurological deficits to invasive electrodes implanted directly into the brain, non-invasive
856 electrophysiology, transcranial magnetic and direct current stimulation, magnetencephalography, and
857 magnetic resonance imaging of a functional, structural or spectroscopic nature. Unfortunately, all of
858 the studies we could find were limited in light of our new framework because only few of them
859 differentiated between the learning processes we outline (Jarosiewicz *et al.*, 2008; Chase, Katz &
860 Schwartz, 2012). Of primary importance, most studies did not measure or control the participants’
861 explicit intended movement. This means that the movement goal of the participant can vary
862 substantially from one trial to the next without the experimenter’s knowledge. Instead of attributing
863 the resulting changes in behavior to an explicit change in the intended movement, it is instead
864 interpreted as arising from implicit learning or noise. This muddies the water tremendously, as implicit
865 and explicit learning occurs in parallel and the brain areas that should be involved in these two types
866 of processes should be quite different (McDougle et al. 2016; Taylor and Ivry 2012, 2014). This means

867 that these studies will misclassify brain activity related to explicit strategy use. It is therefore no small
868 wonder that brain areas commonly implicated in cognitive control and high-level decision making are
869 often observed to be active during in sensorimotor adaptation (Anguera et al. 2010; Cassady et al.
870 2017; Ruitenberg et al. 2018; Seidler and Noll 2008; Shadmehr and Holcomb 1997).

871 Aside from the conflation of implicit and explicit processes, studies on the neural basis of sensorimotor
872 adaptation face a substantial data analysis issue that we believe our framework can help resolve.
873 Namely, the composite error, learning, and movement kinematics over the course of an adaptation
874 experiment are all highly correlated with each other (Diedrichsen et al. 2005; Krakauer et al. 2004;
875 Schlerf et al. 2012). We believe that the errors and processes we have outlined can be decoupled from
876 one another, especially if model-based experiment designs are employed that maximize differences
877 in the predicted operation of these processes. Some studies have started down this path with
878 neurological patients, but many more studies using a variety of methods are needed (Butcher et al.
879 2017; Jahani et al. 2020; Morehead et al. 2017; Wong et al. 2019). As an example, post-movement
880 event-related synchronization was first thought to be a function of (sensory) prediction-error (Tan et
881 al. 2014) but later experiments with better control to differentiate between error types demonstrated
882 that it was linked to performance error (experiment 2 in Torrecillos et al. 2015). We believe model-
883 based designs that include errors and putative learning processes as regressors can help tremendously
884 with these and similar issues.

885 [Extending behavioral methods beyond humans](#)

886 As illustrated above, future research on the neural basis of sensorimotor adaptation would greatly
887 benefit from a discrimination between the types of error and types of learning that we have outlined,
888 both explicit and implicit. The methods that have been developed to parse these errors and processes
889 were developed for use with humans, and many rely heavily on verbal instructions, precluding their
890 direct use with animal models. This seems to present a substantial challenge, but we believe it is
891 possible to translate many existing methods to animal models, such as non-human primates, monkeys,
892 and rodents. Our suggestions here should apply to both experiments on visuomotor and force field
893 adaptation.

894 First, it is important to note that explicit aiming is driven by performance error. Manipulations that
895 affect the expected utility of a given movement strategy should therefore affect the use of explicit
896 strategies. For animal experiments, the most promising method to manipulate performance error
897 independently of sensory prediction-error may be that of Leow and colleagues (2018), where the
898 target either jumps into or out of the path of the reach on every trial. This jumping target either always
899 results in a miss or a hit, irrespective of the participant's movement and sensory prediction-errors.
900 This target jump method could be applied in the context of reaches or joystick tasks. In chimpanzees,
901 a similar manipulation has been shown to modulate feedback corrections as a function of a
902 visuomotor perturbation's the task-relevance, although the focus of this study was not on
903 sensorimotor learning (Kaneko and Tomonaga 2014). Similarly, the sensorimotor perturbation
904 schedule itself can be manipulated, from fully inconsistent (zero-mean random) to fully consistent
905 (blocked or alternating), where strategy use should scale from zero to full (Avraham et al. 2019; Hutter
906 and Taylor 2018). Such task manipulations can be paired with delivery or withholding of rewards, or
907 fully decoupled, but experimenters should carefully consider the performance error implications of
908 direct rewards and punishments, especially on the strategic component of the task (Galea et al. 2015).
909 Manipulation of the expected utility with the above methods can be combined with external sensory
910 cues that are associated with various reward and/or perturbation conditions, as cue-action-outcome
911 associations are easily acquired and are a reliable method for animals to induce a switch in behavioral
912 strategies (Balleine and O'Doherty 2010; Sharpe et al. 2019; Skinner 1938). Conversely, external

913 sensory cues have little or no capacity to modulate implicit sensory prediction-error driven learning
914 over the short term (Cunningham and Welch 1994; Howard et al. 2013; Morehead et al. 2015;
915 Vandevorde and Orban de Xivry 2019, 2020a).

916 The preceding suggestions for animal experiments relate to the control of explicit strategies, but
917 implicit adaptation can also be further broken down into subtypes. The measurement and
918 characterization of temporally labile implicit adaptation is straightforward, as delays between trials
919 will cause this learning to decay (Sing et al. 2009; Zhou et al. 2017). This learning can be measured
920 precisely by the introduction of random delays of differing lengths, coupled with repeated retraining
921 adaptation to asymptotic learning. Temporally stable learning can be dissociated into sensory
922 prediction-error and intrinsic performance error adaptation by the target jump method of Leow *et al.*
923 (2018). This method should induce greater implicit adaptation for enforced target miss over enforced
924 target hit conditions. We believe that some clever experiments could result from the combination of
925 these methods, or others, and we hope to see experimental designs employed in animal studies that
926 discriminate between errors and learning processes that we have described for sensorimotor
927 adaptation.

928 [Beyond traditional motor control](#)

929 Brain-machine interfaces (BMI) are an alternative approach to study the neural control of movement.
930 These techniques record neural activity directly and use it as an electronic control input (Fetz 1969;
931 Vidal 1973) to interact directly with computers, robotic limbs or other devices (Carmena et al. 2003;
932 Hochberg et al. 2006, 2012; Velliste et al. 2008). Here we focus on invasive BMI, where electrodes are
933 implanted directly into the brain. This method is particularly elegant because the experimenter
934 defines the relationship between neural activity and control signals, typically determining subsequent
935 sensory feedback as well (Gilja et al. 2012). In a way, this is an advantage over traditional motor
936 control, where the relationship between neural activity and movements is not fully understood.
937 However, good control with BMI is not a given, as most systems require a substantial amount of
938 training to achieve even mediocre performance (Farshchian et al. 2019; Ganguly and Carmena 2009;
939 Orsborn et al. 2014; Pandarinath et al. 2017).

940 This extended training to enable BMI control means that it is fundamentally a sensorimotor learning
941 problem. It also means that, like in other forms of skill learning, an approach that makes use of our
942 schema could inform the theory behind its application. Performance errors in BMI control are very
943 similar to visuomotor adaptation: this can be the difference between the intended and actual motion
944 of the cursor, or it could be conveyed by points, sounds, or direct rewards and punishments, and so
945 on. If our schema is anything to go by, performance errors may drive changes in the explicit aiming for
946 BMI users. Interestingly, re-aiming has been a concern for some BMI researchers studying adaptation
947 to decoder perturbations, and they have detailed how such a cognitive strategy would affect neural
948 activity (Chase et al. 2012; Jarosiewicz et al. 2008; Zhou et al. 2019). Indeed, these non-human primate
949 studies found clear evidence of re-aiming, which accounted for the majority of their learning in
950 response to decoder perturbations. Human BMI studies also anecdotally report changes in movement
951 strategy during learning: “The participant reported that... she was re-aiming to different directions to
952 compensate for the applied perturbation...” (Sakellaridi et al. 2019). Importantly, although some BMI
953 researchers take re-aiming and other cognitive strategies seriously, this is not the norm, and we
954 believe that it should be.

955 Performance error drives explicit corrections, but BMI learning could be an ideal method to test
956 whether it also drives implicit learning processes, as has generally been thought for skill learning.
957 Indeed, it should be possible to contrast performance error with a putative sensory prediction-error

958 in these tasks. It is as of yet unclear whether sensory predictions exist in BMI control, but their role in
959 *de novo* learning has long been theorized, and these models should provide a rationale for detecting
960 their presence or absence (Jordan and Rumelhart 1992). Temporally labile adaptation should also be
961 fairly straightforward to test. Importantly, the advantage of invasive BMI control is that motor learning
962 models could potentially predict the precise contribution of each neural unit to errors and model the
963 role of each learning process in updating the activity of each neural unit.

964 Beyond the current data: outlook

965 Our framework is built from visuomotor adaptation experiment results that have accumulated in
966 recent years. While we believe this framework has explanatory power in many contexts, it also
967 highlights a number of areas where the motor learning field is missing crucial information to fully
968 understand motor adaptation. Some of these unknowns seem to perennially elude the field, while
969 others are newfound questions that might be answered in a straightforward manner.

970 One particular issue relates to the specific types of internal models that are involved in sensorimotor
971 adaptation. We have been careful to avoid attributing implicit learning in adaptation directly to a
972 control policy (inverse model), or to a forward model. We believe that the currently available data
973 cannot sufficiently rule out learning in either type of model, and it may be that adaptation arises from
974 a modification of both types of model. We believe it is a real possibility that control policy and forward
975 model modification are separate processes that learn at different rates, and potentially from different
976 error signals. This is not altogether much different from the discussions around performance error and
977 sensory prediction-error in Jordan & Rumelhart's original 1992 paper about these error signals and
978 learning processes. Similar to our uncertainty about the specific internal models driving implicit
979 adaptation, we do not believe current data can specify which errors drive adaptation of inverse or
980 forward models. This is mostly because the majority of past experiments have not differentiated
981 between these error signals. These questions are of prime importance in moving the motor learning
982 field forward.

983 Our framework incorporates several learning processes that we believe learn independently.
984 Importantly, in asserting that these are independent, we mean that there are no documented
985 interactions between these processes where the action of one process has unambiguously been
986 shown to modulate that of another learning process. Rather, there is only evidence of indirect
987 interactions, where one process changes factors like the locus of aim, or the amount of performance
988 error, which in turn changes the inputs for a second learning process. In both cases, the actions of one
989 process ultimately affects the behavior of another, but there is an important causal distinction
990 between the two circumstances. We have detailed interactions of these processes in a limited number
991 of contexts such as generalization, but there are many other ways that they could interact that depend
992 on the task design.

993 It would be helpful to have a better understanding of the interactions between the adaptation
994 processes we have outlined. For instance, it is clear that implicit learning, driven by a sensory
995 prediction-error, can cause a performance error, which in turn drives explicit corrections (Mazzoni and
996 Krakauer 2006; Miyamoto et al. 2020; Taylor and Ivry 2011). However, we know little from these
997 studies about the role of target hitting error and temporally labile adaptation. We can model what
998 these processes might do in the context of participants using a specifically provided aiming strategy,
999 but it would be much better to have measurements of these processes in the midst of these complex
1000 tasks settings where implicit and explicit processes are in tension.

1001 Similar to interactions between processes, it has been noted that the methods used to measure
1002 different adapted processes may lead to different results (Maresch et al. 2020b). We believe that more
1003 research in this vein is necessary, as subtle differences in experimental methods may also influence
1004 the processes we have outlined in different ways. For instance, the time required to give verbal
1005 instructions not to aim can cause the entire contribution of implicit temporally labile adaptation to
1006 decay. Although the intended experimental effect of these instructions is to eliminate the use of
1007 explicit strategies, its measured effect will also include the decay of implicit learning. Therefore, to
1008 avoid conflating these effects the verbal instruction group requires comparison to a control group that
1009 waits the same amount of time but receives no instructions to stop aiming.

1010 Given the complexity of the interactions between learning processes, it is difficult to predict their
1011 behavior without a model. To point, we used models to make the learning schematics in this review
1012 and believe formal modelling work will be very helpful for designing experiments to measure these
1013 processes. It is, of course, crucial that this learning be modeled with the appropriate error signals, but
1014 it is equally important that these processes may learn from errors in different ways. Specifically, the
1015 internal learning mechanisms of explicit and implicit adaptation are likely quite different, but there
1016 may also be differences in how the implicit processes we outlined learn. Explicit learning should be
1017 broadly similar to other decision-making and reward learning models, using the performance error
1018 history to select from strategies based on their expected utility (Dayan and Daw 2008). Implicit
1019 learning is likely similar to state-space motor learning models (Cheng and Sabes 2006; Smith et al.
1020 2006; Thoroughman and Shadmehr 2000), but with differences in error how errors map to corrections.
1021 For instance, the target hitting error from target hits and misses appears to be a binary signal (Kim et
1022 al. 2019) and sensitivity to sensory prediction-errors is non-monotonic (Kim et al. 2018).

1023 In the past, modeling efforts for adaptation have primarily used the overall composite error as a
1024 unitary signal driving learning, even for models with more than one learning process (Cheng and Sabes
1025 2006; Smith et al. 2006; Tanaka et al. 2012; Thoroughman and Shadmehr 2000). We believe this has
1026 obscured interesting questions of how performance errors, sensory prediction-errors, and intrinsic
1027 performance errors evolve over time. As discussed previously, a target hit may result in the elimination
1028 of both performance error and intrinsic performance error, but a putative sensory prediction-error
1029 remains, which will still drive adaptation (Mazzoni and Krakauer 2006; Shadmehr et al. 2010; Taylor
1030 and Ivry 2011). It is unclear how sensory prediction-errors evolve over the course of adaptation,
1031 despite the clear prediction from theory that it should be eliminated by forward model adaptation
1032 (Jordan and Rumelhart 1992). The paucity of experimental measures of sensory prediction-errors in
1033 sensorimotor adaptation is astounding, given its prominence in theoretical explanations of behavior.
1034 We believe studies focused on this and other errors could reveal a great deal about the operation of
1035 the motor system.

1036 Model-based insights into the mechanisms of adaptation will not only be useful for process-level
1037 descriptions of this learning, but also for understanding its neurophysiological basis. Given the
1038 diversity of learning processes and errors, it is likely that sensorimotor adaptation recruits a wide
1039 number of brain regions. Although the cerebellum likely plays a prominent role in many facets of
1040 adaptation (both explicit and implicit) it is not the only brain area involved and is likely not the most
1041 important for some of these learning processes. Posterior Parietal, orbitofrontal, dorsolateral
1042 prefrontal and mediolateral prefrontal cortex may play a prominent role in explicit strategy use. These
1043 brain areas have been shown to be involved during sensorimotor adaptation (Diedrichsen et al. 2005;
1044 Shadmehr and Holcomb 1997; Taylor and Ivry 2014), but their specific attribution to explicit and
1045 implicit adaptation remains to be delineated. Although we believe both target hitting error-driven
1046 implicit adaptation and temporally labile adaptation are likely to be learning processes in the motor

1047 stage of our control diagram, we do not have any information to divine their specific neural locus. This
1048 leaves much room for exciting research on the neural basis of sensorimotor adaptation.

1049 Conclusion

1050 We propose a wholistic framework for the understanding and interpretation of sensorimotor
1051 adaptation experiments. Our framework is primarily built from the last decade of observations made
1052 in the domain of visuomotor adaptation. This framework highlights the complexity of the myriad
1053 possible interactions between these processes during the course of typical and non-typical adaptation
1054 experiments. We view this complexity as an asset, rather than a liability. These errors and processes
1055 are distinct, and if care is taken, can be measured, modeled, and understood. The fact that these
1056 different errors and processes can be decorrelated presents a great opportunity to relate them to
1057 neural measurements. Visuomotor adaptation therefore features a tractable complexity, and there is
1058 still a great deal that we can come to understand about this form of learning. Importantly, as a field
1059 we are lucky that the cognitive strategies used in response to visuomotor rotations tend to be uniform
1060 and straightforward to measure. This simple fact opened the door to asking which errors drive which
1061 processes. By integrating these ideas with other observations, we have come to a new picture that
1062 explains several commonly observed effects in visuomotor adaptation experiments. It can and should
1063 be extended to explain even more.

1064 Visuomotor adaptation can serve as a model for other forms of learning specifically because it has the
1065 right mix of simplicity and complexity. There are obvious parallels for other forms of sensorimotor
1066 adaptation, where the exact same learning processes may be operative, perhaps only differing in
1067 proportion. However, the motivating principles behind our framework can be applied more broadly
1068 to the acquisition of arbitrary skills from everyday life, such as darts, touch typing, billiards or tennis.
1069 By understanding the errors that serve as learning signals, and the processes that might learn from
1070 these errors, we may be able to move beyond simple learning curves to an understanding of the web
1071 of subskills contributing to a complex skill. We hope that we have succeeded not only in stimulating
1072 further research on visuomotor adaptation, but also on the broader application of the general
1073 approach we employed in developing our new framework for visuomotor adaptation.

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1665 Figure Captions

1666 Figure 1. Errors in Visuomotor Adaptation Task Contexts. A) A traditional visuomotor rotation task.
1667 The hand of the participant, hidden from view, moves from a start position to the target (black circle).
1668 During baseline, the feedback cursor (white circle), shows the actual location of the hand. When
1669 feedback is perturbed, the position of the cursor is rotated around the start position, so that it moves
1670 in a different direction from the hand when a movement is made away from the center. Later in
1671 learning, the participant has altered the direction of movement to counteract the rotation of
1672 feedback, bringing the cursor closer to the target (asymptotic learning). The difference between the
1673 cursor and target angle (in pink), is the error signal driving learning in most models of motor learning.
1674 We refer to this error as the composite error. B) The change in movement direction that counteracts
1675 the cursor rotation can be made implicitly or explicitly. Experiments that measure or control explicit
1676 aiming strategies reveal that these two types of correction are driven by at least two error signals:
1677 explicit strategies by performance error and implicit adaptation by sensory prediction-error. The
1678 aiming direction is represented by the A symbol within a circle on the right panel. The task
1679 performance error (in orange) is the difference in angle between the target and the cursor. The
1680 sensory prediction-error (cyan) is the difference between the aiming direction and the direction of the
1681 cursor. C) Performance error in visuomotor adaptation is more than a visuospatial error vector
1682 between the cursor and target. On a hit it may include any signal that conveys information about task
1683 success, including a visual “explosion” of the target, a pleasant sound and/or numerical points
1684 provided after the movement. For a miss, the target may not explode, the sound may be unpleasant
1685 and/or points could be withheld or subtracted. These signals of success may accompany or take the
1686 place of visual feedback of position. Performance error may best be thought of as a feature vector
1687 made up of many disparate elements from sensory and cognitive modalities. D) Sensory prediction-
1688 errors are ostensibly generated when sensory feedback is compared to that predicted from the motor
1689 command by a forward model. Here we show a visual signal that is thought to generate such an error,
1690 isolated from performance errors with the task-irrelevant clamped feedback method. Here the cursor
1691 always moves at a fixed angle that is offset from the target, and participants are informed that they
1692 cannot control the direction of this feedback. Moreover, they are instructed not to try to control the
1693 feedback and to instead ignore it while always moving their unseen hand directly to the target. This
1694 manipulation induces implicit adaptation without any changes in aim or performance error
1695 throughout the task. Notably, because the clamped feedback angle is fixed and aim is always at the
1696 target, the putative sensory prediction-error also remains unchanged throughout the task. E) Another
1697 way to isolate adaptation to a sensory prediction-error is to randomly change the sign of performance
1698 error on every trial by jumping the reach target out of the way during the second half of movement.
1699 This allows trial-to-trial measurement of the same implicit adaptation as task-irrelevant clamped
1700 feedback without giving participants information on the nature of the perturbation or providing
1701 specific strategies to ignore or aim to a location. There should be no net change in aim in this task over
1702 the course of a learning block or within a group of participants as the sign of the jumps is random. The
1703 target can also be jumped directly into the path of the cursor so that the movement is always
1704 successful. F) The angular deviation of the feedback is fixed with the task-irrelevant feedback method,
1705 and at small offsets this may intersect the target if it is large (blue circle, Big target hit) or miss the
1706 target when it is small (red circle, small target miss). Along with the target jumping method on the left,
1707 this method revealed that there is a third signal, a seemingly binary target hitting error, that modulates
1708 implicit adaptation even when it is irrelevant to task performance.

1709 Figure 2: Time course of distinct processes hypothesized to underlie visuomotor adaptation. A) Single
1710 process. When a visuomotor rotation is introduced at the end of baseline, the motor system adapts
1711 the direction of the hand’s motion (grey curve) towards the ideal total adaptive response (black

1712 trace), which is the opposite of the feedback rotation angle. This change in hand direction over the
1713 course of trials represents the total adaptive response. Upon removal of the perturbation (washout
1714 period), the adaptation response returns gradually to baseline levels. B) Fast and slow processes. The
1715 total adaptation response can be decomposed into a fast process that learns fast but forgets rapidly
1716 (green curve) and a slow process that evolves slowly but has good retention properties (blue curve).
1717 During washout the fast process takes negative values in order to bring the total adaptation curve to
1718 baseline levels as fast as possible. C) Explicit and implicit processes. The total adaptive response can
1719 be decomposed into an explicit and an implicit process (red and blue curves, respectively). At the start
1720 of the perturbation period, the explicit process is extremely variable and can take positive and
1721 negative values as the participant is experiments with different strategies to cope with the
1722 perturbation. In contrast, the implicit process evolves more slowly and monotonically. During the
1723 washout, participants are instructed to aim their movement directly to the target (often without
1724 feedback) so that the implicit process can be measured directly. The implicit curve during the rotation
1725 is not measured, but estimated by subtracting reported aim from the measured reach direction. C)
1726 Labile and stable processes. The processes underlying motor adaptation can be defined as a function
1727 of their resistance to the passage of time. In this case, interspersing 1-minute breaks throughout the
1728 experiment allows one to look at the effect of time on the adaptation response. Two processes emerge
1729 from this manipulation: a stable process whose response does not decay during one-minute breaks
1730 and a labile process that decays substantially during these breaks. The labile process appears to learn
1731 to both learn and forget faster than the stable process. E) Error-specific implicit process. Implicit
1732 adaptation to a putative sensory prediction-error differs depending on whether the target was hit by
1733 the cursor or not. Specifically, there is less adaptation when the target is hit. Therefore, it has been
1734 hypothesized that the implicit adaptation response could be divided into a sensory prediction-error
1735 (SPE) driven and a target hitting error (THE) driven process (blue and cyan curves, respectively). F)
1736 Reward learning process. In the absence of any visuospatial feedback about the participant's
1737 performance, the adaptive response can be guided by reward signals such as binary feedback (with
1738 gradual perturbation) or with graded feedback (e.g. points, a tone) that varies relative the distance
1739 from ideal behavior. In this case, learning is extremely variable but slowly evolves towards the ideal
1740 correction for the imposed perturbation.

1741 Figure 3. Schematic model for generating goal directed reaching movements and the locus of learning
1742 in visuomotor adaptation tasks. The control diagram is composed of non-motor and a motor stages.
1743 The motor stage contains all the elements of the conventional motor control scheme: it interacts with
1744 the environment via a body that is controlled by motor commands. Noisy sensory information about
1745 the state of the body is fed back to the motor system with a delay. This sensory information is
1746 integrated with the output of a forward model that uses an efference copy of the motor commands
1747 to predict the current and future state of the body. The motor commands are determined by the
1748 control policy (sometimes refer to as inverse model), which takes the loss function and the state
1749 estimate of the body as input and generates motor commands as an output. Optimal feedback control
1750 proposes that the motor commands result from the minimization of the loss function. In our schema,
1751 the loss function represents the interface between the motor and non-motor stages. The loss function
1752 is shaped by the non-motor part of the system in function of task requirements (instructed speed,
1753 accuracy demands, etc.) and internal factors such as motivation or vigor. These factors are not only
1754 sensitive to verbal instructions and apparent task conditions but also "high level" cognitive insight.
1755 Plasticity in this schematic model is represented by the colored arrows. The task performance error is
1756 computed at the level of the non-motor stage based on sensory feedback while the sensory
1757 prediction-error is computed in the motor stage based on the output of the forward model and the
1758 sensory feedback. We hypothesized that the sensory prediction-error could update both the forward

1759 model and control policy. Performance error primarily shapes the loss function but may also directly
1760 update the control policy.

1761 Figure 4. How the processes of visuomotor adaptation contribute to behavior during learning. A) Trial-
1762 by-trial evolution of the different processes during the adaptation period and washout in the presence
1763 of 1-minute breaks (grey vertical lines). Four important time points are highlighted and further
1764 described in panels B-I. The positive aiming peak corresponds to the trial where the aiming direction
1765 was furthest in counterclockwise direction. Implicit build-up corresponds to a time point early in
1766 perturbation block where implicit adaptation is small relative to the adjustment from explicit aim.
1767 Asymptotic learning corresponds to the end of the adaptation period where total adaptation is at its
1768 maximum. The negative aiming peak corresponds to the moment early in washout where the aiming
1769 direction is maximally clockwise. In this simulation, the participant aims at in the direction that will
1770 lead to best performance throughout the task. Note that the processes sum, although we have shown
1771 them each relative to zero. B-E) The internal generalization of implicit adaptation (SPE-implicit, THE-
1772 implicit and labile implicit) at the four time points highlighted above. The state of each process is
1773 represented across different possible movement directions (x-axis) relative to the visual target
1774 (vertical black dotted line). This shows the amount of implicit adaptation that is be predicted if the
1775 participant chose to aim for anywhere other than where they did. These curves show a peak of implicit
1776 generalization shifts with the point of explicit aim and that the implicit adaptation that is sampled on
1777 a given trial also depends on the explicit aim. Therefore, shifts in aim can cause a substantial change
1778 in the expressed amount implicit adaptation (change from D to E). F-I) Here, the effect of implicit
1779 adaptation (gray wedge) upon a given aimed reach is shown within the task workspace. The bar graphs
1780 show a breakdown of the total implicit adaptation (grey bars) into its constituent components (dark
1781 blue: SPE-implicit, cyan: THE-implicit, green: labile implicit). Notably, at the negative aiming peak, both
1782 the aim and labile learning are opposing the aftereffects caused by the temporally stable implicit
1783 adaptation.

1784 Figure 5. Specific cases where multiple learning processes can be misunderstood. First Row: control
1785 or measurement of explicit aim is critical for measuring an implicit aftereffect. A) Effect of instruction
1786 on total adaptation measured during a retention period (grey rectangle) in the absence of any visual
1787 feedback. The dotted curve illustrates differences in retention that have been observed in many
1788 experiments. B and C) illustrate how a simple change in aim can lead to the solid or dotted gray lines
1789 observed in A). Importantly, only aim has changed over these two simulations, but they can be
1790 misinterpreted as a difference in retention of an implicit motor memory if aim is not measured or
1791 controlled. Red, dark blue, cyan and green correspond, respectively, to the explicit, SPE-implicit, THE-
1792 implicit and labile implicit processes. SPE: sensory prediction-error; THE: target hitting error. Second
1793 Row: Savings upon relearning occurs because explicit aiming strategies are re-engaged during
1794 relearning. D) Evolution of the different processes underlying adaptation during learning and
1795 relearning. E) Same as D but learning and relearning are superimposed. Solid line: processes during
1796 learning; Dotted lines: processes during relearning. G) breakdown of total adaptation into the
1797 subprocesses for the first trials of the learning (left) and of the relearning (right) periods. Third Row:
1798 Hypothesized response for each component of motor adaptation at different error sizes. The x-axis
1799 provides the perturbation size while the y-axis reflects the amount of adaptation. The height of each
1800 layer represents the amount of adaptation from each of the processes. The sum of all the layers gives
1801 the total adaptation response to a specific error.

1802