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1 **Perceptual learning alters post-sensory processing in human decision making**

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12

13 **Abstract**

14 An emerging view in perceptual learning is that improvements in perceptual sensitivity
15 are not only due to enhancements in early sensory representations but also due to
16 changes in post-sensory decision processing. In humans, however, direct
17 neurobiological evidence of the latter account remains scarce. Here, we trained
18 participants on a visual categorization task over three days and used multivariate pattern
19 analysis of the electroencephalogram to identify two temporally-specific components
20 encoding *sensory* (Early) and *decision* (Late) evidence, respectively. Importantly, the
21 single-trial amplitudes of the Late, but not the Early component, were amplified in the
22 course of training and these enhancements predicted the behavioural improvements on
23 the task. Correspondingly, we modelled these improvements with a reinforcement
24 learning mechanism, using a reward prediction error signal to strengthen the readout of
25 sensory evidence used for the decision. We validated this mechanism through a robust
26 association between the model's decision variables and our Late component's
27 amplitudes indexing decision evidence.

28

29 **Introduction**

30 Consider an image intelligence analyst inspecting a large array of noisy CCTV or
31 satellite images in order to identify targets that might pose a real security threat. Her
32 ability to perform this task successfully depends on her years of experience in
33 interpreting such images. This example highlights that training and experience are
34 required to induce long-lasting improvements in our ability to make decisions based on
35 ambiguous sensory information a phenomenon commonly referred to as perceptual
36 learning ^{1,2}. Despite the prevalence and obvious utility of this phenomenon in everyday
37 life (e.g. learning in an ever-changing environment to make better predictions and plan
38 future actions), its neural substrates and how these affect decision-making remain
39 elusive.

40

41 Several psychophysical studies offered evidence linking perceptual learning with
42 enhancements in early sensory representations ³⁻⁹ and with changes in post-sensory
43 processing relating to attention and decision making ¹⁰⁻¹². In line with the latter account
44 (i.e. late influences), recent experimental work in non-human primates (NHP) ^{13,14} offered
45 compelling evidence that perceptual learning in decision making can affect how early
46 sensory representations are interpreted downstream by higher-level areas to form a
47 decision.

48

49 Correspondingly, recent functional magnetic resonance imaging (fMRI) experiments in
50 humans started to address the question of whether perceptual learning affects later
51 processing stages ¹⁵⁻¹⁸. To date, however, little has been done to exploit *time-resolved*
52 electrophysiological signatures that can accurately differentiate between early stimulus
53 encoding and late decision-related processing. Here, we test the extent to which
54 perceptual learning alters post-sensory encoding of decision evidence in humans by

55 recording electroencephalography (EEG) data during a face/car perceptual
56 discrimination experiment (Fig. 1a) over the course of three days. Previously, using this
57 task and single-trial multivariate discriminant analysis of the EEG we identified two
58 temporally distinct neuronal components that discriminated between the stimulus
59 categories: an Early component that occurred around 170 ms after stimulus presentation
60 and a Late component that occurred around 300 ms post-stimulus ¹⁹⁻²³.

61

62 We showed that compared to the Early one, the Late component was a better predictor
63 of behaviour ²⁰, it systematically shifted later in time with perceived task difficulty ¹⁹ and it
64 was a significantly better predictor of trial-by-trial changes in the rate of evidence
65 accumulation (i.e. drift rate) in a drift diffusion model ^{19,23}. Finally, while the Early
66 component amplitudes remained unaffected when the same (face/car) stimuli were
67 coloured red or green and the task was switched to colour discrimination those of the
68 Late component were reduced almost to zero ^{19,22,23}. Taken together these findings
69 indicated that the Early component encodes the incoming sensory evidence, whereas
70 the Late component indexes, post-sensory, decision-relevant evidence. These previous
71 findings are intriguing because they establish a benchmark against which to evaluate the
72 extent to which perceptual learning influences earlier vs. later stages of decision making.

73

74 Specifically, here we test how activity associated with each of these Early and Late EEG
75 components is affected by training. We hypothesize that if perceptual learning primarily
76 alters post-sensory encoding of decision evidence, discrimination performance for our
77 Late but not the Early component should systematically increase across the three
78 training sessions. Similarly, as perceptual sensitivity improves with training we expect
79 the Late component to move earlier in time, reflecting a decrease in perceived task
80 difficulty. Moreover, our ability to exploit single-trial variability in the EEG will offer a

81 mechanistic characterization of these effects by establishing whether improvements in
82 discrimination are a result of gain modulation (i.e. amplification of the differential
83 response) of the component amplitudes, a reduction in the trial-to-trial variability (i.e.
84 noise) of the component amplitudes or both.

85

86 Finally, we explore the possibility that these improvements can be understood in terms
87 of a reinforcement learning (RL) mechanism^{14,17,24-26}, whereby the connections between
88 early and late decision processing stages are strengthened via a reward prediction error,
89 gradually enhancing the readout of relevant information and leading to improved
90 perceptual sensitivity.

91

92 **Results**

93 We collected behavioural and EEG data from 14 participants during a speeded face vs.
94 car categorization task using noisy stimuli that varied in the amount of available sensory
95 evidence (i.e. phase coherence of the stimuli). Visual feedback was provided for each
96 response prior to the presentation of the next stimulus (Fig. 1a). Participants performed
97 the same task on three consecutive days. Using a mixed-effects logistic regression
98 analysis, we found that accuracy was significantly improved ($\chi^2_{df=1} = 19.37$, $p < 0.001$,
99 Fig. 1b) over the three training days. Using a mixed-effects linear regression analysis,
100 we found that reaction times (RT) were significantly reduced over the three training days
101 ($\chi^2_{df=1} = 8.92$, $p < 0.003$, Fig. 1c). We note that, as expected, we also found a main
102 effect of stimulus difficulty, with accuracy increasing ($\chi^2_{df=1} = 28.08$, $p < 0.001$) and RT
103 decreasing ($\chi^2_{df=1} = 21.24$, $p < 0.001$) with the amount of sensory evidence, respectively.
104 There was no interaction between the amount of sensory evidence and training day on
105 either measure (accuracy: $\chi^2_{df=1} = 0.16$, $p = 0.68$, RT: $\chi^2_{df=1} = 0.383$, $p = 0.54$).

106

107 Next, we sought to identify the Early (sensory) and Late (decision-related) EEG
108 components that discriminate between face and car trials and investigate how these are
109 affected by training. To this end, we used a single-trial multivariate discriminant analysis
110 ^{27,28} to identify linear spatial weightings of the EEG sensors, which best discriminated
111 between the two trial types. For each participant, we estimated, within short pre-defined
112 time windows of interest, a projection in the multidimensional EEG space (i.e. a spatial
113 filter) that maximally discriminated between the two categories on stimulus-locked data
114 (Eq. 1; see Methods). Applying this spatial filter to single-trial data produced a
115 measurement of the resultant discriminating component amplitude (henceforth y).
116 Component amplitudes can be thought of as indexing the quality of the evidence in each
117 trial, in that a high positive amplitude reflects an easy face trial, an amplitude near zero
118 reflects a difficult trial, and a high negative amplitude reflects an easy car trial (Fig. 2a).
119 We used the area under a receiver operating characteristic curve (i.e. Az-value) with a
120 leave-one-out trial cross validation procedure to quantify the discriminator's performance
121 (i.e. the degree of separation in the single-trial amplitude distributions associated with
122 each stimulus category).

123

124 Our discriminator's performance as a function of stimulus-locked time revealed the
125 presence of two temporally specific components (Fig. 2b; Early, mean peak time: 187
126 ms; Late, mean peak time: 431 ms), consistent with our previous work ¹⁹⁻²³. Most
127 crucially, even though both the Early and Late components reliably discriminated
128 between image categories, only the discrimination performance for our Late component
129 appeared to systematically increase across the three training days. To formally test for
130 this effect we extracted subject-specific peak Az-values for each of the Early and Late
131 components and run a mixed-effects linear regression analysis with training day,

132 component (i.e. Early vs Late) and their interaction as separate predictors. We found a
133 significant main effect of training day ($x_{df=1}^2 = 7.61$, $p = 0.006$), a main effect of
134 component ($x_{df=1}^2 = 5.0371$, $p = 0.025$) and a significant interaction between the two
135 ($x_{df=1}^2 = 7.46$, $p = 0.006$), indicating that discriminator performance for the Late
136 component increased systematically across training days, whereas that of the Early
137 component remained unchanged (Fig. 2c). Taken together, these results provide
138 compelling evidence that it is primarily the encoding of the decision evidence in the Late
139 component, rather than the sensory evidence in the Early component, that is being
140 enhanced in the course of training.

141

142 In previous work ²⁰, we showed that, unlike the Early component, the peak time of the
143 Late component moved later in time as perceived task difficulty increased, consistent
144 with longer integration times for more difficult decisions ²⁹⁻³¹. Here, we exploit this finding
145 to provide additional evidence linking the Late component with the process of learning.
146 Specifically, we hypothesized that the latency of the Late component should move
147 earlier in time as learning unfolds (i.e. as choices become easier). Using a separate
148 mixed-effects linear regression analysis we found a significant main effect of training day
149 ($x_{df=1}^2 = 21.56$, $p < 0.001$), a main effect of component ($x_{df=1}^2 = 51.3$, $p < 0.001$;) and a
150 significant interaction of the two ($x_{df=1}^2 = 51.75$, $p < 0.001$) on component peak times,
151 indicating that the Late component peak times were reduced systematically across
152 training days, whereas those of the Early component remained unchanged (Fig. 2d).
153 These findings reinforce the notion that it is the temporal dynamics of the Late decision-
154 related component that change as a function of training.

155

156 To better understand the mechanism by which improvements in discrimination

157 performance for the Late component came about, we capitalized on the single-trial
158 variability in the component amplitudes. Specifically, we tested whether there was an
159 increase in the distance between the mean face and car component amplitudes in the
160 Late component ($\bar{y}_f - \bar{y}_c$; Fig. 3a), a reduction in the trial-by-trial variability around those
161 means ($\sigma(y_{c,f})$; Fig. 3b) or a combination of both. We ran a mixed-effects linear
162 regression analysis, with the amount of sensory evidence, training days, and their
163 interaction as separate predictors.

164

165 As expected from previous findings^{20,22,23} we found a main effect of the amount of
166 sensory evidence on the means ($x_{df=1}^2 = 11.52$, $p < 0.001$, Fig. 3c) but not on the
167 variance of these component amplitudes ($x_{df=1}^2 = 0.38$, $p = 0.53$, Fig. 3d). Crucial to this
168 work, we also found a main effect of training day on the mean responses ($x_{df=1}^2 = 6.72$, p
169 $= 0.009$, Fig. 3c), but not on the variance of these component amplitudes ($x_{df=1}^2 = 2.76$, p
170 $= 0.1$, Fig. 3d). No significant interaction effects of sensory evidence and training day
171 were observed ($x_{df=1}^2 = 0.03$, $p = 0.86$ and $x_{df=1}^2 = 0.25$, $p = 0.61$, means and variance
172 respectively). These results suggest that the improvements in discrimination
173 performance for the Late component over the course of training are primarily the result
174 of gain modulation (i.e. enhanced sensory readout leading to amplification of the
175 differential response) of the component amplitudes rather than a reduction in the trial-to-
176 trial variability in these amplitudes.

177

178 To establish a concrete link between our EEG component amplitudes and improvements
179 in behaviour we ran a separate logistic regression analysis whereby trial-by-trial changes
180 in the amplitudes (i.e. y 's) of the Early and Late components over all training days were
181 used to predict participants' choices on individual trials (i.e. face choice probability,

182 coded as 1 (0) for face (car) choices, respectively). Using the resulting subject-specific
183 regression coefficients we found that our Late component was both a reliable predictor
184 of participants' choices (t-test, $t(13) = 11.52$, $p < 0.001$) and a significantly better
185 predictor compared to the Early component (paired t-test, $t(13) = 2.949$, $p = 0.011$).

186

187 Though the novelty of our work rests primarily with the EEG results, we also test the
188 view that the observed perceptual improvements in behaviour might involve a RL-like
189 mechanism similar to that proposed for reward-based learning^{14,17,26,32}. To this end, we
190 modelled our participants' choices using a RL model (see Methods). In brief, the model
191 makes choices based on a decision variable (DV), with positive values indicating a
192 higher likelihood of a face choice and negative values indicating a higher likelihood of a
193 car choice. The DV reflects the representational strength of the presented stimulus on a
194 given trial and corresponds to the stimulus sensory evidence scaled by the absolute
195 difference between its signal weight and a noise weight for the antagonistic stimulus.
196 Whilst the role of the former is to enhance the sensory read-out of the presented
197 stimulus, the latter captures the extent to which the antagonistic stimulus interferes with
198 the processing of the available sensory evidence.

199

200 In the RL framework employed here these weights are updated by means of a prediction
201 error signal, which quantifies the discrepancy between the expected and actual value of
202 the decision outcome on each trial. To account for the possibility that signal and noise
203 weights may be differentially updated the prediction error signal is scaled by separate
204 learning rates in each of the two weight updates. The mechanism of this update is such
205 that on a given trial a correct choice will always lead to an increase of the chosen
206 stimulus signal weight and to a decrease of the unchosen stimulus noise weight, yielding
207 enhanced signal to noise ratio for the correctly chosen stimulus. Crucially this update is

208 also scaled by the chosen stimulus representation, which exerts a further consolidating
209 effect on perceptual learning (see Methods).

210

211 We fit the model to individual participant data and found a highly significant
212 correspondence between the model's accuracy predictions and actual behaviour ($r =$
213 0.882 , $p < 0.001$ – Fig. 4a). We also compared the model with two competing
214 alternatives (i.e. a model with signal and noise weights updated with only one learning
215 rate and a model with only a single perceptual weight) using Bayesian Model Selection
216 (BMS) that accounts for inter-subject variability by treating each model as a random
217 effect. We found that our model provided a better fit to the observed choice behaviour
218 (see Methods and Figure 4a). Consistent with an enhanced readout of sensory evidence
219 we observed a subject-wise gradual build-up in the trial-by-trial estimates of the signal
220 weights mirrored by a gradual decrease in the noise weight estimates (e.g. Fig. 4b and
221 4c respectively). Between-day comparisons (1 vs. 2 and 2 vs. 3) of subject-wise mean
222 DVs (Fig. 4d; paired t-test: $t_{1vs2}(13) = -6.77$ $p < 0.001$; $t_{2vs3}(13) = -2.36$ $p = 0.02$) and
223 aggregate perceptual weights (Fig. 4e; signal weights: paired t-test: $t_{1vs2}(13) = -6.74$ $p <$
224 0.001 ; $t_{2vs3}(13) = -2.36$ $p = 0.02$; noise weights: paired t-test: $t_{1vs2}(13) = 6.74$ $p < 0.001$;
225 $t_{2vs3}(13) = 2.35$ $p = 0.02$) revealed a significant effect of learning as observed in
226 behaviour.

227

228 To offer neurobiological validity to the model we performed two additional analyses.
229 Firstly, we correlated the single-trial DVs estimated by the model with our EEG
230 component amplitudes. We predicted that if the brain computes a version of our model-
231 based DVs to drive choices then one should observe a systematic amplification of the
232 DV with training and a significant correlation with our Late EEG component shown to
233 index decision evidence. To this end we ran another regression analysis whereby the

234 single-trial amplitudes of our Early and Late components were used to predict the
235 model's DVs. We found that our Late component was both a reliable predictor of the
236 model's DVs (Fig. 4f; t-test, $t(13) = 21.81$, $p < 0.001$) and a significantly better predictor
237 than the Early component (Fig. 4f; paired t-test, $t(13) = 3.06$, $p = 0.009$).

238

239 Secondly, we separated our trials into four bins (quartiles) based on the model-predicted
240 magnitudes of the prediction error (PE) signal, which is thought to guide learning. We
241 then ran a single-trial discriminant analysis on feedback-locked EEG data between the
242 very low and very high PE trial groups (i.e. we kept the middle two quartiles as “test”
243 data – see below). This analysis revealed a centroparietal EEG component peaking on
244 average at 354ms post-feedback (Fig. 5a). The timing and topography of this component
245 are consistent with previous work on feedback-related processing in the human brain
246 using a probabilistic reinforcement learning task^{33,34}.

247

248 To formally test whether this EEG component was parametrically modulated by the
249 magnitude of the PE signal, we computed discriminator amplitudes (y) for trials with
250 intermediate magnitude levels (i.e. those left out from the original discrimination
251 analysis). Specifically, we applied the spatial filter of the window that resulted in the
252 highest discrimination performance for the extreme PE magnitude levels to the EEG
253 data with intermediate values. We expected these “unseen” trials would show a
254 parametric response profile such that the resulting mean component amplitude at the
255 time of peak discrimination would proceed from very low < low < high < very high PE
256 magnitude. Using this approach, we demonstrated that the mean discriminator output for
257 each quartile increased as a function of the model's PE magnitude (all pair-wise t-test
258 comparisons across adjacent trial groups: P values < 0.001; Fig. 5b), thereby
259 establishing a concrete link between the model's PE estimates and our feedback-related

260 EEG component. Taken together, these findings provide further evidence that perceptual
261 learning enhances decision-related evidence, likely via a RL-like mechanism.

262

263 **Discussion**

264

265 In this work, we offer the evidence from time-resolved electrophysiological signals in
266 humans linking perceptual learning with post-sensory processing during a perceptual
267 categorization task. Specifically, we showed that improvements in behavioural
268 performance were accompanied primarily by late enhancements in decision-related
269 evidence. In particular, we demonstrated that single-trial amplitudes of a late EEG
270 component indexing decision evidence^{19,20,23,35} were amplified in the course of learning,
271 such that these representations became more robust to noise (rather than a reduction in
272 noise as such). In contrast a temporally earlier component encoding sensory (stimulus)
273 evidence – even in the absence of a face/car decision task¹⁹ – was not affected by
274 training. These findings suggest that it is the strengthening of the connections between
275 early sensory encoding and downstream decision-related processing that are driving
276 perceptual learning in our task.

277

278 Crucially, we also showed that the onset of the late component (which on average
279 coincides with the onset of decision evidence accumulation³⁶⁻³⁸) systematically moves
280 earlier in time with training. This finding is particularly interesting since we have
281 previously observed comparable temporal shifts in this component while manipulating
282 task/stimulus difficulty^{19,20,23}. We view this as additional evidence that our learning
283 effects on the late component lead to changes in perceptual sensitivity. More
284 specifically, the earlier the onset time of the late component the stronger the behavioural
285 improvements, consistent with a decrease in perceived task difficulty. These temporal

286 changes are also in line with a faster and more efficient accumulation of evidence as
287 often predicted by sequential sampling models of decision making²⁹⁻³¹ (e.g. increases in
288 the drift-rate and decrease in nondecision time variability).

289

290 Consistent with previous accounts^{14,17} we also showed that these learning-induced
291 behavioural improvements could be reliably explained in terms of a RL mechanism (see,
292 e.g.,³⁹). More specifically, we showed that a model that uses a prediction error signal
293^{24,25,40,41} to continuously adjust the stimulus specific perceptual weights on the sensory
294 evidence²⁶ led to amplification of the relevant stimulus representations in the course of
295 training (i.e. making them more robust to noise). We further demonstrated that trial-by-
296 trial changes in our Late EEG component shown to index decision evidence reliably
297 tracked the amplification of sensory information predicted by the model. These results
298 imply that perceptual learning involves an enhanced readout of sensory information
299 during decision making likely via a RL-like process, endorsing the view of a domain-
300 general learning mechanism²⁴. It is worth noting that whilst it is true that our task did not
301 involve any explicit reward as a reinforcer, we view the implicit rewarding nature
302 associated with correct responses as a “teaching signal” for strengthening the neural
303 representation of sensory contingencies²⁶.

304

305 Research on perceptual learning has recently focused on the extent to which perceptual
306 learning is due to improvements in sensory abilities that are (informationally and
307 temporally) earlier than the decision process itself or due to improvements in post-
308 sensory and decision-related processing. Consistent with the former account, several
309 psychophysics studies have demonstrated that perceptual learning is often highly
310 specific to the location and other properties of the stimuli³⁻⁹, implying specificity to the
311 trained retinal location^{42,43}. Similarly human fMRI studies offered evidence of activity

312 enhancements in retinotopic areas corresponding to the trained visual fields ⁴⁴ and
313 increased responses along the whole hierarchy of early visual areas that correlated with
314 improvements in behavioural performance following training over the course of several
315 weeks ^{45,46}. These results are further corroborated by EEG recordings in humans
316 showing post-training improvements in early visually-evoked components over occipital
317 electrode sites ⁴⁷⁻⁴⁹ and electrophysiological recordings in NHPs linking behavioural
318 performance with improvements in perceptual sensitivity in primary sensory areas ⁵⁰⁻⁵².

319

320 In contrast, other psychophysical studies proposed that perceptual learning can also
321 arise from changes in how sensory signals are read out or interpreted by decision-
322 making mechanisms ^{32,53,54} rather than from changes in primary sensory areas as such.
323 Neural evidence in support of this interpretation comes from NHP electrophysiology
324 studies ^{13,14}, demonstrating that perceptual learning on a motion discrimination task
325 affects downstream decision accumulator areas, rather than regions encoding the
326 sensory evidence (i.e. motion direction). Specifically, accumulator neurons improved
327 responsiveness to the decision evidence in the course of learning (as reflected in
328 steeper evidence accumulation slopes), with these improvements being proportional to
329 the animals' performance on the task. Correspondingly, recent fMRI studies in humans
330 started to explore the effect of learning on the activity and connectivity patterns of
331 higher-level ventral temporal ^{55,56} and decision-related regions ¹⁵⁻¹⁸.

332

333 These seemingly discrepant accounts of the temporal locus of perceptual learning may
334 be reconciled by considering differences in the experimental demands of the task at
335 hand. For example, a recent theoretical account proposed a unified two-stage model of
336 perceptual learning ⁵⁷⁻⁵⁹. According to this model, there are two distinct types of plasticity
337 underlying perceptual learning: feature-based plasticity and task-based plasticity. On the

338 one hand, feature based plasticity affects early sensory processing stages and occurs
339 with mere exposure to stimuli, regardless of whether the stimuli are relevant to the task
340 or not. Task-based plasticity, on the other hand, can be thought of as a higher-level
341 processing stage arising from direct and active involvement in a behavioural task. In this
342 formulation, the relative contribution of the two plasticity types to the overall
343 enhancement in performance hinges largely on the training procedures, the stimuli and
344 the intricacies of the task used in learning ⁶⁰.

345

346 More specifically, a distinction could be drawn between tasks that involve learning of
347 relatively primitive stimulus features such as orientation, spatial frequency or contrast
348 and those employing more complex stimuli such as objects and faces ⁵⁹. Although
349 learning of highly primitive features could occur locally at the level of early sensory
350 processing, more complex stimuli (made up of a combination of primitive features) might
351 require active involvement of downstream higher-level sensory or decision-related areas.
352 In our design, for instance, complex object categories are used and phase
353 discrimination, which is shown to involve processes beyond early visual cortex ⁶¹, is
354 required to perform the task reliably. As such, our findings appear to rely heavily on the
355 enhancement of the relevant stimulus representations during post-sensory, rather than
356 early sensory processing.

357

358 In summary, our study provides critical insights into the neurobiology of perceptual
359 learning and offers strong support to the notion that neuronal plasticity can occur at
360 multiple time-scales and locations, depending on task demands and context. As such
361 our findings can help revise existing theories of perceptual learning focusing only on
362 early sensory processing and provide the foundation upon which future studies continue
363 to interrogate the neural systems underlying perceptual decision making.

364

365 **Methods**

366 **Participants**

367 Fourteen subjects (7 female and 7 male, age range 23-28 years) participated in this
368 study. All were right handed, had normal or corrected-to-normal vision and reported no
369 history of neurological problems. The study was approved by the College of Science and
370 Engineering Ethics Committee at the University of Glasgow (CSE01353) and informed
371 consent was obtained from all participants.

372

373 **Stimuli**

374 We used a set of 18 face and 18 car images (image size 512 x 512 pixels, 8-bits/pixel),
375 adapted from our previous experiments ^{19,20}. Face images were selected from the Face
376 Database of the Max Planck Institute of Biological Cybernetics ⁶² and car images were
377 sources from the internet. Both image types contained equal numbers of frontal and side
378 views (up to $\pm 45^\circ$). All images were equated for spatial frequency, luminance and
379 contrast and they all had identical magnitude spectra (average magnitude spectrum of
380 all images in the database). We manipulated the phase spectra of the images using the
381 weighted mean phase ⁶³ technique to change the amount of sensory evidence in the
382 stimuli as characterized by their % phase coherence. We selected two levels of sensory
383 evidence for this study (32.5% and 37.5 % phase coherence) that are known to yield
384 performance spanning psychophysical threshold, based on our previous studies ^{19,20}. A
385 Dell Precision Workstation (Intel Core 2 Quad) running Windows 7 (64 bit) with an ATI
386 FirePro 2270 graphics card and PsychoPy 1.8 presentation software ⁶⁴ controlled the
387 stimulus display. Images were presented on a Dell 2001FP TFT monitor (resolution,
388 1600x1200 pixels; refresh rate, 60 Hz). Subjects were positioned 75cm from the monitor
389 and each image subtended approximately 6 x 6 degrees of visual angle.

390

391 **Behavioural task**

392 Subjects performed a simple image categorization task whereby they had to classify an
393 image either as a face or car. The stimulus was presented for 50 ms and subjects were
394 asked to make a response as soon as they had formed a decision, with a response
395 deadline set at 1.25 s. Subjects indicated their decision with a button press on a
396 response device (Cedrus RB-740) using their right index and middle fingers for a face
397 and a car response, respectively. Subjects received visual feedback following each
398 response that lasted for 500 ms. A tick and a cross were presented for a correct and an
399 incorrect response, respectively (subtended 0.7 x 0.7 degrees of visual angle). A cross
400 was also shown when subjects failed to make a response within the pre-allocated
401 duration of 1.25 s following the stimulus. Feedback was followed by an inter-trial interval
402 that varied randomly in the range between 1 – 1.5 s. There were a total of 288 trials
403 (divided equally between the two image categories and the two levels of sensory
404 evidence), presented in 4 blocks of 72 trials with a 60 s rest period between each block.
405 The entire experiment lasted approximately 20 minutes. Each subject performed this
406 task on three consecutive days, with the experiment taking place at the same time on
407 each day. On the first day, subjects performed a short practice session of the face/car
408 categorization task with high % phase coherence stimuli (50%) to familiarize themselves
409 with the structure and pace of the task.

410

411 **EEG data acquisition**

412 EEG was collected inside an electrostatically shielded booth using a 64-channel EEG
413 amplifier system (BrainAmps MR-Plus, Brain Products, Germany) and recorded using
414 Brain Vision Recorder (BVR; Version 1.10, Brain Products, Germany) with a 1000 Hz
415 sampling rate and an analogue bandpass filter of 0.016-250 Hz. The EEG cap consisted

416 of a 64 Ag/AgCl actiCAP electrodes (Brain Products, Germany) positioned according to
417 the international 10–20 system of electrode positioning. The ground electrode was
418 embedded in the EEG cap and placed along the midline between electrode Pz and Oz.
419 The reference electrode was placed on the left mastoid. All input impedances were kept
420 below 10 kΩ. For each participant, an effort was made to position the EEG cap in a
421 consistent manner across the three training days, by keeping the distance between
422 electrodes and certain anatomical landmarks (i.e. outer canthi, inion, nasion) constant.
423 Experimental event codes and button responses were also synchronized with the EEG
424 data and collected using the BVR software.

425

426 **EEG pre-processing**

427 We performed basic pre-processing of the EEG signals offline using Matlab (Mathworks,
428 Natick, MA). Specifically, we applied a 0.5 Hz high-pass filter to remove DC drifts, and
429 100 Hz low pass filter to remove high frequency artefacts not associated with
430 neurophysiological processes. These filters were applied together, non-causally to avoid
431 distortions caused by phase delays (using MATLAB “filtfilt”). The EEG data was
432 additionally re-referenced to the average of all channels.

433

434 **Eye-movement artefact removal**

435 Prior to the main experiment, we asked our participants to complete an eye movement
436 calibration task during which they were instructed to blink repeatedly upon the
437 appearance of a fixation cross in the centre of the screen and then to make several
438 horizontal and vertical saccades according to the position of the fixation cross. The
439 fixation cross subtended 0.4 x 0.4 degrees of visual angle. Horizontal saccades
440 subtended 15 degrees and vertical saccades subtended 10 degrees. This exercise
441 enabled us to determine linear EEG sensor weightings corresponding to eye blinks and

442 saccades (using principal component analysis) such that these components were
443 projected onto the broadband data from the main task and subtracted out ²⁷.

444

445 **Single-trial discriminant analysis**

446 To discriminate between face and car trials we applied a linear multivariate classifier to
447 stimulus-locked EEG data, using the sliding window approach we used in previous work
448 (e.g., ^{20,65}). Specifically, we identified a projection of the multichannel EEG signal, $\mathbf{x}_i(t)$,
449 where $i = [1 \dots T]$ and T is the total number of trials, within a short time window that
450 maximally discriminated between the two stimulus categories. All time windows had a
451 width of $N = 50$ ms and the window centre τ was shifted from -100 to 1000 ms relative to
452 stimulus onset, in 10 ms increments. More specifically, we used logistic regression ²⁷ to
453 learn a 64-channel spatial weighting, $\mathbf{w}(\tau)$, that achieved maximal discrimination at each
454 time window, arriving at the one-dimensional projection $y_i(\tau)$, for each trial i and a given
455 window τ :

456

$$457 \quad y_i(\tau) = \frac{1}{N} \sum_{t=\tau-N/2}^{t=\tau+N/2} \mathbf{w}(\tau)^\perp \mathbf{x}_i(t) \quad (1)$$

458

459 where \perp is used to indicate the transpose operator. Note that our classifier is designed to
460 return activity from processes that help maximize the difference across the two
461 conditions of interest while minimizing the effect of processes common to both
462 conditions. In doing so the classifier tries to map positive and negative discriminant
463 component amplitudes (i.e. $y_i(\tau)$) to face and car trials, respectively. In other words,
464 large positive values indicate a higher likelihood of a face stimulus, large negative values
465 a higher likelihood of a car stimulus and values near zero reflect more difficult stimuli
466 (see Fig. 2a for an example). This procedure in effect scales the resulting discriminating

467 component amplitudes in a manner that is directly comparable across the three training
468 days. The same discrimination procedure was also applied on feedback-locked data to
469 discriminate between trials with low versus high prediction error magnitudes (as
470 estimated by our model – see below).

471

472 We quantified the performance of the discriminator at each time window using the area
473 under a receiver operating characteristic (ROC) curve, referred to as an A_z -value, using
474 a leave-one-out trial procedure⁶⁶. Furthermore we used a bootstrapping technique to
475 assess the significance of the discriminator by performing the leave-one-out test after
476 randomizing the trial labels. We repeated this randomization procedure 1000 times to
477 produce a probability distribution for A_z , and estimated the A_z value leading to a
478 significance level of $p < 0.01$.

479

480 Given the linearity of our model we also computed scalp topographies of the
481 discriminating components resulting from Eq. 1 by estimating a forward model as:

482

$$483 \quad a(\tau) = \frac{x(\tau)y(\tau)}{y(\tau)^\perp y(\tau)} \quad (2)$$

484

485 where $y_i(\tau)$ is now organized as a vector $y(\tau)$, where each row is from trial i , and $x_i(t)$ is
486 organized as a matrix, $x(\tau)$, where rows are channels and columns are trials, all for time
487 window τ . These forward models can be viewed as scalp plots and interpreted as the
488 coupling between the discriminating components and the observed EEG²⁷.

489

490 **Single-trial regression analyses**

491 To analyse the behavioural and neural data resulting from our EEG discrimination

492 analysis we use a mixed-effects general linear modelling (GLM) approach. These GLM
493 models are similar to repeated-measures ANOVA models but they offer a better account
494 for inter-subject response variability (by incorporating subjects as a random effect) and
495 allow the mixing of both continuous and categorical variables^{67,68}. Details of the
496 dependent and predictor variables used for each regression analysis are given in the
497 main text. The significance of a predictor variable or set of variables is tested using a
498 log-likelihood ratio test, whereby the log-likelihood of the model with all predictors is
499 compared to the log-likelihood of the model without the predictors being tested. The
500 difference in the log-likelihood of two models is distributed according to a χ^2 distribution
501 whose degrees of freedom equal the difference in the number of parameters in the two
502 models. We fit these mixed-effects models using the lme4 package
503 (<http://cran.rproject.org/web/packages/lme4/index.html>) using R ([http://www.r-](http://www.r-project.org)
504 [project.org](http://www.r-project.org)). We note that repeating these analyses using a conventional ANOVA
505 approach yielded virtually identical results, further highlighting the robustness of our
506 effects.

507

508 To demonstrate that our Late EEG component was a better predictor of behaviour
509 compared to the Early one, we ran a separate logistic regression analysis. Specifically,
510 for each participant the trial-by-trial discriminant amplitudes (y 's) for the two components
511 (over all training days) were used as separate regressors to predict each participant's
512 face choice probabilities ($P(f)$) on individual trials (i.e. $P(f) = 1$ [0] for face [car] choices)
513 as:

514

$$515 \quad P(f) = 1/(1 + e^{-[\beta_0 + \beta_1 y_{Early} + \beta_2 y_{Late}]}) \quad (3)$$

516

517 Then, to establish a more reliable trial-by-trial association between Late brain activity
518 and choice behaviour, we tested: 1) whether the Late regression coefficients across
519 subjects (β_2 's) come from a distribution with mean greater than zero (using an one
520 sample *t-test*) and 2) whether the Late regression coefficients across subjects (β_2 's)
521 come from a distribution with mean greater than those of the Early one (β_1 's) (using a
522 paired *t-test*). For all analyses, we provide exact p values where possible, but values
523 below 10^{-3} are abbreviated as such (i.e. $p < 0.001$).

524

525 **Reinforcement learning model**

526 We used a variant of the Rescorla-Wagner reinforcement learning model to account for
527 perceptual improvements in the course of learning ^{14,17,26}. In this model perceptual
528 decisions are driven by a decision variable (*DV*) denoting the subject's hidden
529 representations of sensory contingencies (i.e. association between sensory evidence
530 and stimulus category). The strength of such representations is modulated via dynamic
531 updates of category specific perceptual weights based on feedback information, thereby
532 accounting for potential differences in learning trajectories between the stimulus
533 categories. Indeed, compared to previous work that used a single stimulus-invariant
534 perceptual weight ^{14,17} the introduction of category-specific perceptual weights is
535 designed to capture subject-wise choice biases in that, subjects might have a choice
536 bias towards cars or faces and likewise might display an increasing ability to recognize
537 cars or faces throughout the task.

538

539 Moreover, our perceptual weights comprise signal and noise weights. Whilst the former
540 is designated to enhance stimulus representation in the course of learning, the latter
541 accounts for the interference exerted by the antagonistic stimulus against the acquisition
542 of the correct sensory contingencies. Thus, in our model perceptual learning is expected

543 to occur via gradually increasing signal weights as well as gradually decreasing noise
544 weights. Compared to previous RL-like perceptual models^{14,17}, this better captures
545 instances whereby improved task performance depends both on greater ability to
546 recognize a given stimulus as well as greater ability to rule out the antagonistic stimulus.
547 In other words on a face trial subjects might correctly choose face partly because they
548 are able to identify face-like features and partly because they are able to recognize that
549 there are no car-like features.

550

551 More specifically, on each trial i decision activities specific to each stimulus category
552 ($A_{stim}, stim \in \{face, car\}$) were estimated as the stimulus specific sensory evidence
553 (E_{stim}) scaled by the absolute difference between the stimulus specific signal weight
554 (v_{stim}) and the noise weight of the antagonistic stimulus ($n_{\setminus stim}$):

555

$$556 \quad A_{face}^i = E_{face}^i |v_{face}^i - n_{car}^i|$$

$$557 \quad A_{car}^i = E_{car}^i |v_{car}^i - n_{face}^i| \tag{4}$$

558

559 As perceptual learning progresses, the estimates of signal and noise weights grow apart
560 and so does their distance (i.e. absolute difference) on the real line. As a result, the
561 read-out of sensory evidence is increasingly enhanced reflecting the improving ability to
562 discriminate between perceptual stimuli in the course of training.

563

564 Whilst the magnitude of E_{stim} was defined according to the percentage of phase
565 coherence in the stimulus (0.325 and 0.375 for low and high coherence trials
566 respectively), its sign was related to stimulus category (positive for faces and negative
567 for cars). This ensured decision activities to be a signed quantity, whose magnitude

568 tracked the time-varying strength of stimulus representation.

569

570 Trial-by-trial estimates of the DV were computed based on the decision activity of the
571 presented stimulus:

572

$$573 \quad DV^i = A_{stim}^i \quad (5)$$

574

575 Note that the DV too is a signed quantity with positive values indicating a higher
576 likelihood of a face choice and negative values indicating a higher likelihood of a car
577 choice and as such is directly comparable with the sign of our EEG discriminator
578 component amplitudes y . Correspondingly, both the model's DV s and our component
579 amplitudes are orthogonal to potentially confounding quantities such as task (stimulus)
580 difficulty, decision confidence (or uncertainty) and expected value, all of which covary
581 with the absolute value of the DV and y (i.e. both high positive and high negative DV and
582 y values correspond to easier, more confident and thereby higher expected value
583 choices).

584

585 Subject-wise DV trajectories were then mapped to choice propensities (i.e. probabilities)
586 using a sigmoid function:

587

$$588 \quad P_{face}^i = \sigma(\beta(DV^i)) \quad (6)$$

589

590 where $\sigma(z) = 1/(1 + e^{-z})$ is the sigmoid function and β the inverse of the temperature
591 representing the degree of stochasticity in the decision function. Next, the expected
592 value (EV) of the outcome on the same trial was computed based on the modulus

593 (absolute value) of the DV as: $EV^i = \sigma(\beta(|DV^i|))$. In other words, whilst high positive
 594 and high negative DV values (subjectively easier choices) increase the EV of the
 595 outcome (and therefore the expected probability of being rewarded), values near zero
 596 (subjectively difficult choices) reduce it.

597

598 Finally, on each trial, given reward feedback r (coded as 1 and 0 for reward and no
 599 reward respectively), perceptual weights were updated via a prediction error signal,
 600 $\delta^i = r^i - EV^i$, which quantified the degree of deviation between the actual and expected
 601 outcome, scaled by a learning rate parameter α and an associativity component
 602 ($E_{stim}^i A_{choice}^i$) whose role was to dynamically modulate the updating of perceptual
 603 weights depending on the strength of sensory evidence (E_{stim}) and strength of the
 604 chosen stimulus representation (A_{choice}):

605

$$\begin{aligned}
 606 \quad v_{choice}^{i+1} &= v_{choice}^i + \alpha \delta^i E_{choice}^i A_{choice}^i \\
 607 \quad n_{\backslash choice}^{i+1} &= n_{\backslash choice}^i + \alpha \delta^i E_{\backslash choice}^i A_{choice}^i
 \end{aligned} \tag{7}$$

608

609 where subscript $\backslash choice$ indicates the unchosen stimulus. Note that the signal weight of
 610 the unchosen stimulus and the noise weight of the chosen stimulus were not updated.
 611 The sign of the update was determined by the prediction error so that whilst correct
 612 choice trials resulted in an increase of signal weights and a decrease of noise weights,
 613 incorrect choice trials had an opposite effect on the updating of perceptual weights. For
 614 example on a face trial whilst a correct face choice would result in an increase of v_{face}
 615 and a reduction of n_{car} an incorrect car choice would yield an increase of n_{car} and a
 616 reduction of v_{face} . Moreover, the learning/unlearning of correct/incorrect sensory
 617 contingencies underpinned by this dynamic updating of perceptual weights was further

618 facilitated by the strength of the stimulus representation A_{choice} . In other words, the
619 stronger the stimulus representation the greater the impact of the prediction error on
620 perceptual learning (via the updating of perceptual weights) and vice versa.

621

622 We fitted two variants of this model, one with a single learning rate and one with two
623 different learning rates for the signal and noise weights' updates, respectively. The latter
624 model allowed for the possibility that signal and noise weights may be differentially
625 updated therefore probing subject-specific biases in perceptual information processing.
626 In other words, whilst some subjects might boost the signal to noise ratio for a given
627 stimulus by primarily enhancing signal weights, others might achieve the same result by
628 primarily reducing noise weights. Whilst the total number of free parameters in the first
629 variant of the model was four (v^1, n^1, β, α) the number of free parameters in the second
630 variant was five ($v^1, n^1, \beta, \alpha_{face}, \alpha_{car}$) where v^1, n^1 represent the initial perceptual
631 weights' estimates (i.e. on the first trial) for face and car stimuli. In addition, we also fitted
632 a simple perceptual RL model (as described in ^{14,17}), whereby the read-out of sensory
633 evidence was scaled only by a signal weight and the trial-by-trial updating of this signal
634 weight was driven by a prediction error computed as previously illustrated. The number
635 of free parameters in this model was four ($v^1, bias, \beta, \alpha$) where *bias* represents the
636 indecision point in the choice sigmoid function.

637

638 **Model fitting procedure and model comparison**

639 In order to prevent overfitting, for each subject i we found the *maximum a posteriori*
640 estimate of the model free parameters:

641

$$642 \theta_i^{MAP} = \operatorname{argmax}_{\theta} p(C_i | \theta_i) p(\theta_i | \xi) \quad (8)$$

643

644 where $p(C_i|\theta_i)$ is the cross-entropy loss function between empirical and predicted
645 choices C_i given the model parameters θ_i and $p(\theta_i|\xi)$ is the prior distribution on the
646 model parameters θ_i given the population-level hyperparameters ξ . Priors were defined
647 as normal distributions $N(\mu, \sigma)$ where μ was sampled from a normal distribution with
648 mean 0 and standard deviation 1 and σ was set to 1e2. To preserve the parameters'
649 natural bounds, $\log(\beta)$ and $\text{logit}(\alpha)$ transforms of the parameters were implemented.

650

651 We subsequently performed formal Bayesian model comparison between the 3 models
652 to determine the one that best fitted our behavioural data. This approach treats each
653 model as a random-effect at the between subject-level and therefore is more robust to
654 outliers than fixed-effect approaches⁶⁹. Specifically, we first estimated the subject-wise
655 Laplace approximated log evidence for each model. We subsequently computed the
656 model-wise exceedance probability (i.e. how confident we are that a model is more likely
657 than any other model tested) using SPM8's `spm_BMS` routine⁷⁰. We found that the
658 exceedance probability of the model with 2 learning rates ($\varphi = 0.88$) was greater than
659 those of the model with a single learning rate ($\varphi = 0.11$) and with a single perceptual
660 weight ($\varphi = 0.001$) (see inset Fig. 4a).

661

662 To assess the model's goodness of fit we plotted the subject-wise empirical choice
663 accuracy against the model's predicted accuracy for different days and stimulus phase
664 coherence levels. Additionally, we tested whether subject-wise model's mean *DVs* and
665 perceptual weights significantly increased over training as observed with behavioural
666 performance.

667

668 **Data availability**

669 The data that support the findings of this study are available from the corresponding
670 author upon request.

671

672

References

673

674 1 Gilbert, C. D., Sigman, M. & Crist, R. E. The neural basis of
675 perceptual learning. *Neuron* **31**, 681-697 (2001).

676 2 Goldstone, R. L. Perceptual learning. *Annual review of psychology*
677 **49**, 585-612, doi:10.1146/annurev.psych.49.1.585 (1998).

678 3 Ball, K. & Sekuler, R. Direction-specific improvement in motion
679 discrimination. *Vision research* **27**, 953-965 (1987).

680 4 Crist, R. E., Kapadia, M. K., Westheimer, G. & Gilbert, C. D.
681 Perceptual learning of spatial localization: Specificity for
682 orientation, position, and context. *Journal of Neurophysiology*
683 **78**, 2889-2894 (1997).

684 5 Fahle, M. & Edelman, S. Long-term learning in vernier acuity:
685 Effects of stimulus orientation, range and of feedback. *Vision*
686 *research* **33**, 397-412 (1993).

687 6 Fiorentini, A. & Berardi, N. Perceptual learning specific for
688 orientation and spatial frequency. *Nature* (1980).

689 7 Karni, A. & Sagi, D. Where practice makes perfect in texture
690 discrimination: evidence for primary visual cortex plasticity.
691 *Proceedings of the National Academy of Sciences* **88**, 4966-4970
692 (1991).

693 8 Poggio, T., Fahle, M. & Edelman, S. Fast perceptual learning in
694 visual hyperacuity. *Science* **256**, 1018-1021 (1992).

695 9 Sagi, D. & Tanne, D. Perceptual learning: learning to see.
696 *Current opinion in neurobiology* **4**, 195-199 (1994).

697 10 Ahissar, M. & Hochstein, S. Task difficulty and the specificity
698 of perceptual learning. *Nature* **387**, 401-406, doi:10.1038/387401a0
699 (1997).

700 11 Mollon, J. D. & Danilova, M. V. Three remarks on perceptual
701 learning. *Spatial vision* **10**, 51-58 (1996).

702 12 Ahissar, M. & Hochstein, S. Attentional control of early
703 perceptual learning. *Proceedings of the National Academy of*
704 *Sciences of the United States of America* **90**, 5718-5722 (1993).

705 13 Law, C.-T. & Gold, J. I. Neural correlates of perceptual learning
706 in a sensory-motor, but not a sensory, cortical area. *Nature*
707 *neuroscience* **11**, 505-513 (2008).

708 14 Law, C.-T. & Gold, J. I. Reinforcement learning can account for
709 associative and perceptual learning on a visual-decision task.
710 *Nature neuroscience* **12**, 655-663 (2009).

711 15 Baldassarre, A. *et al.* Individual variability in functional
712 connectivity predicts performance of a perceptual task.
713 *Proceedings of the National Academy of Sciences of the United*
714 *States of America* **109**, 3516-3521, doi:10.1073/pnas.1113148109
715 (2012).

716 16 Chen, N. H. *et al.* Sharpened cortical tuning and enhanced
717 cortico-cortical communication contribute to the long-term neural
718 mechanisms of visual motion perceptual learning. *NeuroImage* **115**,
719 17-29, doi:10.1016/j.neuroimage.2015.04.041 (2015).

720 17 Kahnt, T., Grueschow, M., Speck, O. & Haynes, J.-D. Perceptual
721 learning and decision-making in human medial frontal cortex.
722 *Neuron* **70**, 549-559 (2011).

723 18 Lewis, C. M., Baldassarre, A., Comitteri, G., Romani, G. L. &
724 Corbetta, M. Learning sculpts the spontaneous activity of the
725 resting human brain. *Proceedings of the National Academy of*

726 *Sciences of the United States of America* **106**, 17558-17563,
727 doi:10.1073/pnas.0902455106 (2009).

728 19 Philiastides, M. G., Ratcliff, R. & Sajda, P. Neural
729 representation of task difficulty and decision making during
730 perceptual categorization: a timing diagram. *The Journal of*
731 *Neuroscience* **26**, 8965-8975 (2006).

732 20 Philiastides, M. G. & Sajda, P. Temporal characterization of the
733 neural correlates of perceptual decision making in the human
734 brain. *Cerebral cortex* **16**, 509-518 (2006).

735 21 Philiastides, M. G. & Sajda, P. Causal influences in the human
736 brain during face discrimination: a short-window directed
737 transfer function approach. *IEEE transactions on bio-medical*
738 *engineering* **53**, 2602-2605, doi:10.1109/TBME.2006.885122 (2006).

739 22 Philiastides, M. G. & Sajda, P. EEG-informed fMRI reveals
740 spatiotemporal characteristics of perceptual decision making. *The*
741 *Journal of neuroscience : the official journal of the Society for*
742 *Neuroscience* **27**, 13082-13091, doi:10.1523/JNEUROSCI.3540-07.2007
743 (2007).

744 23 Ratcliff, R., Philiastides, M. G. & Sajda, P. Quality of evidence
745 for perceptual decision making is indexed by trial-to-trial
746 variability of the EEG. *Proceedings of the National Academy of*
747 *Sciences* **106**, 6539-6544 (2009).

748 24 Rushworth, M. F., Mars, R. B. & Summerfield, C. General
749 mechanisms for making decisions? *Current opinion in neurobiology*
750 **19**, 75-83 (2009).

751 25 Schultz, W., Dayan, P. & Montague, P. R. A neural substrate of
752 prediction and reward. *Science* **275**, 1593-1599 (1997).

753 26 Guggenmos, M., Wilbertz, G., Hebart, M. N. & Sterzer, P.
754 Mesolimbic confidence signals guide perceptual learning in the
755 absence of external feedback. *eLife* **5**, doi:10.7554/eLife.13388
756 (2016).

757 27 Parra, L. C., Spence, C. D., Gerson, A. D. & Sajda, P. Recipes
758 for the linear analysis of EEG. *NeuroImage* **28**, 326-341,
759 doi:10.1016/j.neuroimage.2005.05.032 (2005).

760 28 Sajda, P., Philiastides, M. G. & Parra, L. C. Single-trial
761 analysis of neuroimaging data: inferring neural networks
762 underlying perceptual decision-making in the human brain. *IEEE*
763 *reviews in biomedical engineering* **2**, 97-109,
764 doi:10.1109/RBME.2009.2034535 (2009).

765 29 Ratcliff, R. & Smith, P. L. Perceptual discrimination in static
766 and dynamic noise: the temporal relation between perceptual
767 encoding and decision making. *Journal of experimental psychology.*
768 *General* **139**, 70-94, doi:10.1037/a0018128 (2010).

769 30 Ratcliff, R., Smith, P. L. & McKoon, G. Modeling Regularities in
770 Response Time and Accuracy Data with the Diffusion Model. *Current*
771 *directions in psychological science* **24**, 458-470,
772 doi:10.1177/0963721415596228 (2015).

773 31 Smith, P. L. & Ratcliff, R. Psychology and neurobiology of simple
774 decisions. *Trends in neurosciences* **27**, 161-168,
775 doi:10.1016/j.tins.2004.01.006 (2004).

776 32 Petrov, A. A., Doshier, B. A. & Lu, Z.-L. The dynamics of
777 perceptual learning: an incremental reweighting model.
778 *Psychological review* **112**, 715 (2005).

779 33 Fouragnan, E., Retzler, C., Mullinger, K. & Philiastides, M. G.
780 Two spatiotemporally distinct value systems shape reward-based

781 learning in the human brain. *Nature communications* **6**, 8107,
782 doi:10.1038/ncomms9107 (2015).

783 34 Philiastides, M. G., Biele, G., Vavatzanidis, N., Kazzer, P. &
784 Heekeren, H. R. Temporal dynamics of prediction error processing
785 during reward-based decision making. *NeuroImage* **53**, 221-232,
786 doi:10.1016/j.neuroimage.2010.05.052 (2010).

787 35 Lou, B., Li, Y., Philiastides, M. G. & Sajda, P. Prestimulus
788 alpha power predicts fidelity of sensory encoding in perceptual
789 decision making. *NeuroImage* **87**, 242-251,
790 doi:10.1016/j.neuroimage.2013.10.041 (2014).

791 36 Kelly, S. P. & O'Connell, R. G. Internal and external influences
792 on the rate of sensory evidence accumulation in the human brain.
793 *The Journal of neuroscience : the official journal of the Society*
794 *for Neuroscience* **33**, 19434-19441, doi:10.1523/JNEUROSCI.3355-
795 13.2013 (2013).

796 37 O'Connell, R. G., Dockree, P. M. & Kelly, S. P. A supramodal
797 accumulation-to-bound signal that determines perceptual decisions
798 in humans. *Nature neuroscience* **15**, 1729-1735, doi:10.1038/nn.3248
799 (2012).

800 38 Philiastides, M. G., Heekeren, H. R. & Sajda, P. Human scalp
801 potentials reflect a mixture of decision-related signals during
802 perceptual choices. *The Journal of neuroscience : the official*
803 *journal of the Society for Neuroscience* **34**, 16877-16889,
804 doi:10.1523/JNEUROSCI.3012-14.2014 (2014).

805 39 Sutton, R. S. & Barto, A. G. *Reinforcement learning: An*
806 *introduction*. (MIT press, 1998).

807 40 O'Doherty, J. P., Dayan, P., Friston, K., Critchley, H. & Dolan,
808 R. J. Temporal difference models and reward-related learning in
809 the human brain. *Neuron* **38**, 329-337 (2003).

810 41 Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J. & Frith,
811 C. D. Dopamine-dependent prediction errors underpin reward-
812 seeking behaviour in humans. *Nature* **442**, 1042-1045 (2006).

813 42 Fahle, M. Perceptual learning: A case for early selection.
814 *Journal of vision* **4**, 4-4 (2004).

815 43 Fahle, M. Perceptual learning: specificity versus generalization.
816 *Current opinion in neurobiology* **15**, 154-160 (2005).

817 44 Schwartz, S., Maquet, P. & Frith, C. Neural correlates of
818 perceptual learning: a functional MRI study of visual texture
819 discrimination. *Proceedings of the National Academy of Sciences*
820 *of the United States of America* **99**, 17137-17142,
821 doi:10.1073/pnas.242414599 (2002).

822 45 Furmanski, C. S., Schluppeck, D. & Engel, S. A. Learning
823 strengthens the response of primary visual cortex to simple
824 patterns. *Current Biology* **14**, 573-578 (2004).

825 46 Jehee, J. F., Ling, S., Swisher, J. D., van Bergen, R. S. & Tong,
826 F. Perceptual learning selectively refines orientation
827 representations in early visual cortex. *The Journal of*
828 *neuroscience* **32**, 16747-16753 (2012).

829 47 Bao, M., Yang, L., Rios, C., He, B. & Engel, S. A. Perceptual
830 learning increases the strength of the earliest signals in visual
831 cortex. *The Journal of neuroscience : the official journal of the*
832 *Society for Neuroscience* **30**, 15080-15084,
833 doi:10.1523/JNEUROSCI.5703-09.2010 (2010).

834 48 Pourtois, G., Rauss, K. S., Vuilleumier, P. & Schwartz, S.
835 Effects of perceptual learning on primary visual cortex activity

836 in humans. *Vision research* **48**, 55-62,
837 doi:10.1016/j.visres.2007.10.027 (2008).

838 49 Censor, N., Bonneh, Y., Arieli, A. & Sagi, D. Early-vision brain
839 responses which predict human visual segmentation and learning.
840 *Journal of vision* **9**, 12 11-19, doi:10.1167/9.4.12 (2009).

841 50 Ghose, G. M., Yang, T. & Maunsell, J. H. Physiological correlates
842 of perceptual learning in monkey V1 and V2. *Journal of*
843 *neurophysiology* **87**, 1867-1888 (2002).

844 51 Schoups, A., Vogels, R., Qian, N. & Orban, G. Practising
845 orientation identification improves orientation coding in V1
846 neurons. *Nature* **412**, 549-553, doi:10.1038/35087601 (2001).

847 52 Yan, Y. et al. Perceptual training continuously refines neuronal
848 population codes in primary visual cortex. *Nature neuroscience*
849 **17**, 1380-1387 (2014).

850 53 Doshier, B. A. & Lu, Z. L. Mechanisms of perceptual learning.
851 *Vision research* **39**, 3197-3221, doi:Doi 10.1016/S0042-
852 6989(99)00059-0 (1999).

853 54 Lu, Z.-L., Liu, J. & Doshier, B. A. Modeling mechanisms of
854 perceptual learning with augmented Hebbian re-weighting. *Vision*
855 *research* **50**, 375-390 (2010).

856 55 Kuai, S.-G., Levi, D. & Kourtzi, Z. Learning optimizes decision
857 templates in the human visual cortex. *Current Biology* **23**, 1799-
858 1804 (2013).

859 56 Li, S., Mayhew, S. D. & Kourtzi, Z. Learning shapes the
860 representation of behavioral choice in the human brain. *Neuron*
861 **62**, 441-452 (2009).

862 57 Shibata, K., Watanabe, T., Sasaki, Y. & Kawato, M. Perceptual
863 learning incepted by decoded fMRI neurofeedback without stimulus
864 presentation. *science* **334**, 1413-1415 (2011).

865 58 Shibata, K., Sagi, D. & Watanabe, T. Two-stage model in
866 perceptual learning: toward a unified theory. *Annals of the New*
867 *York Academy of Sciences* **1316**, 18-28, doi:10.1111/nyas.12419
868 (2014).

869 59 Watanabe, T. & Sasaki, Y. Perceptual learning: toward a
870 comprehensive theory. *Annual review of psychology* **66**, 197-221,
871 doi:10.1146/annurev-psych-010814-015214 (2015).

872 60 Li, W., Piech, V. & Gilbert, C. D. Perceptual learning and top-
873 down influences in primary visual cortex. *Nature neuroscience* **7**,
874 651-657, doi:10.1038/nn1255 (2004).

875 61 Perna, A., Tosetti, M., Montanaro, D. & Morrone, M. C. BOLD
876 response to spatial phase congruency in human brain. *Journal of*
877 *vision* **8**, 15 11-15, doi:10.1167/8.10.15 (2008).

878 62 Troje, N. F. & Bühlhoff, H. H. Face recognition under varying
879 poses: The role of texture and shape. *Vision research* **36**, 1761-
880 1771 (1996).

881 63 Dakin, S. C., Hess, R. F., Ledgeway, T. & Achtman, R. L. What
882 causes non-monotonic tuning of fMRI response to noisy images?
883 *Current biology : CB* **12**, R476-477; author reply R478 (2002).

884 64 Peirce, J. W. PsychoPy—psychophysics software in Python. *Journal*
885 *of neuroscience methods* **162**, 8-13 (2007).

886 65 Gherman, S. & Piliastides, M. G. Neural representations of
887 confidence emerge from the process of decision formation during
888 perceptual choices. *NeuroImage* **106**, 134-143,
889 doi:10.1016/j.neuroimage.2014.11.036 (2015).

890 66 Duda, R. O. & Hart, P. E. *Pattern classification and scene*
891 *analysis*. Vol. 3 (Wiley New York, 1973).
892 67 Baayen, R. H., Davidson, D. J. & Bates, D. M. Mixed-effects
893 modeling with crossed random effects for subjects and items.
894 *Journal of Memory and Language* **59**, 390-412,
895 doi:10.1016/j.jml.2007.12.005 (2008).
896 68 Gelman, A. & Hill, J. *Data analysis using regression and*
897 *multilevel/hierarchical models*. (Cambridge University Press,
898 2006).
899 69 Stephan, K. E. et al. Ten simple rules for dynamic causal
900 modeling. *NeuroImage* **49**, 3099-3109,
901 doi:10.1016/j.neuroimage.2009.11.015 (2010).
902 70 Stephan, K. E., Weiskopf, N., Drysdale, P. M., Robinson, P. A. &
903 Friston, K. J. Comparing hemodynamic models with DCM. *NeuroImage*
904 **38**, 387-401, doi:10.1016/j.neuroimage.2007.07.040 (2007).
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917

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919

920 **Figure Legends**

921

922 **Figure 1.** Experimental design and behaviour. **(a)** Schematic representation of the
923 experimental paradigm. Subjects had to categorize a noisy image presented for 50ms as
924 a face or a car and indicate their choice with a button press within 1250ms following the
925 stimulus presentation. Feedback was then presented for 500ms (a tick or a cross for a
926 correct and an incorrect response, respectively) followed by an inter-stimulus interval
927 (ISI) that varied randomly between 1-1.5s. Subjects performed this task on three
928 consecutive training days. Sample face and car images at the two levels of phase
929 coherence used in the task (32.5% and 37.5%) are shown on the right. **(b)** Proportion of
930 correct choices and **(c)** Mean reaction times (RT) as a function of the three training days
931 (1: blue, 2: green, 3: red) and the two levels of phase coherence of the stimuli, averaged
932 across subjects. Faint lines represent individual subject data. Error bars represent
933 standard errors across subjects.

934

935

936 **Figure 2.** Post-sensory effects of perceptual learning. **(a)** Single-trial discriminator
937 amplitudes (y) for the Early (dotted) and Late (solid) component windows for faces
938 (black) and cars (grey) at 37.5% phase coherence from a representative subject on the
939 third training day. The component amplitudes are shown as histograms on the right, with
940 a cutoff (the thick black line) to separate trials into positive vs. negative amplitudes,
941 indicating a higher likelihood of a face and a car trial, respectively. **(b)** Multivariate
942 discriminator performance (A_z) during face-vs-car outcome discrimination of stimulus-
943 locked EEG responses across the three training days (1: blue, 2: green, 3: red),
944 averaged across subjects, showing the presence of the Early and Late components. The
945 dotted line represents the average A_z value leading to a significance level of $p = 0.01$,

946 estimated using a bootstrap test. Faint lines represent individual subject data. **(c)**
947 Average discriminator performance and scalp topographies for the Early (magenta) and
948 Late (cyan) components across the three training days estimated at time of subject-
949 specific maximum discrimination. Faint lines represent individual subject data. Error bars
950 represent standard errors across subjects. **(d)** Average onset times for the Early
951 (magenta) and Late (cyan) components across the three training days. Faint lines
952 represent individual subject data. Error bars represent standard errors across subjects.

953

954 **Figure 3.** Enhanced readout of post-sensory decision evidence. **(a)** Schematic
955 illustration of possible effects on the distribution of single-trial discriminator amplitudes in
956 the course of learning. Top: increases in the distance between the mean response for
957 faces and cars. Bottom: reduction in the variance of the face and car responses. Both
958 examples lead to a smaller overlap (more separation) between the face and car
959 distributions. **(b)** Changes in the mean distance between the face and car distributions
960 for the Late component across the three training days (1: blue, 2: green, 3: red). **(c)**
961 Changes in the variance of the face and car distributions for the Late component across
962 the three training days. The faint lines in **(b)** and **(c)** represent individual subject data,
963 while the error bars represent standard errors across subjects.

964

965 **Figure 4.** Reinforcement learning model for perceptual choices. **(a)** Scatter plot showing
966 the correlation between the performance of individual subjects and models, over the
967 three training days and the two level of stimulus phase coherence (using the winning
968 model). Inset: exceedance probabilities of three competing models (see Methods for
969 details). **(b)** Individual trial estimates of the model's decision variable (DV) for a
970 representative subject over the course of the three training days, superimposed on the
971 amount of stimulus-defined sensory evidence (black trace). **(c)** Signal (positive) and

972 noise (negative) perceptual weights for faces (solid) and cars (dashed) over the three
973 training days for the same subject shown in **(b)**. **(d)** Average magnitude of the model's
974 DVs across subjects over the course of the three training days. Individual subject data
975 are also shown as point estimates. **(e)** Average signal (positive) and noise (negative)
976 perceptual weights for faces (solid) and cars (faint) over the three training days.
977 Individual subject data are also shown as point estimates. **(f)** Average regression
978 coefficients reflecting the trial-by-trial association between the model's DVs and the
979 amplitudes of the Early and Late EEG components estimated over all training days.
980 Individual subject data are also shown as point estimates.

981

982 **Figure 5.** Electrophysiological correlates of prediction error (PE). **(a)** Multivariate
983 discriminator performance (A_z) during very low versus very high PE magnitude trials on
984 feedback-locked EEG responses averaged across subjects and days revealing a late PE
985 component. Discriminator performance and component peak times were comparable
986 across the three days. The dotted line represents the average A_z value leading to a
987 significance level of $p = 0.01$, estimated using a bootstrap test. Faint lines represent
988 individual subject data. Inset: average scalp topography associated with the PE
989 component, estimated at time of subject-specific maximum discrimination. **(b)** Mean
990 discriminator amplitude (γ) for the PE component, binned in four quartiles based on
991 model-based estimates of the magnitude of the PE, showing a clear parametric
992 response along the four trial groups. Quartiles 1 and 4 were used to train the classifier,
993 while quartiles 2 and 3 contain “unseen” data with intermediate PE magnitude levels.
994 Individual subject data are also shown as point estimates.

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