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Dissociation of Category-Learning Systems via Brain Potentials

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Abstract

Behavioral, neuropsychological, and neuroimaging evidence has suggested that categories can often be learned via either an explicit rule-based mechanism critically dependent on medial temporal and prefrontal brain regions, or via an implicit information-integration mechanism relying on the basal ganglia. In this study, participants viewed sine-wave gratings (i.e., Gabor patches) that varied on two dimensions and learned to categorize them via trial-by-trial feedback. Two different stimulus distributions were used; one was intended to encourage an explicit rule-based process and the other an implicit information-integration process. We monitored brain activity with scalp electroencephalography (EEG) while each participant (1) passively observed stimuli represented of both distributions, (2) categorized stimuli from one distribution, and, one week later, (3) categorized stimuli from the other distribution. Categorization accuracy was similar for the two distributions. Subtractions of Event-Related Potentials (ERPs) for correct and incorrect trials were used to identify neural differences in rule-based and information-integration categorization processes. We identified an occipital brain potential that was differentially modulated by categorization condition accuracy at an early latency (150 - 250 ms), likely reflecting the degree of holistic processing. A stimulus-locked late positive complex associated with explicit memory updating was modulated by accuracy in the rule-based, but not the information-integration task. Likewise, a feedback-locked P300 ERP associated with expectancy was correlated with performance only in the rule-based, but not the information-integration condition. These results provide additional evidence for distinct brain mechanisms supporting rule-based versus implicit information-integration category learning and use.

1. Introductions

Categories, as conceptualized based on perceived regularities, allow us to make sense of, describe, and order our worlds (Rips, Smith, & Medin, 2012). Categories come in many different forms--from categories based on a single feature (e.g., objects that are red) to much more complicated relational concepts (e.g., *chases* or *conduit*). Many have argued that human

47 categorization is not a unitary process, but rather can engage different systems depending on the
48 category structure or the conditions during category learning (e.g., (Ashby & Maddox, 2011;
49 Nomura & Reber, 2008; Seger & Miller, 2010; Smith & Grossman, 2008; Yamauchi &
50 Markman, 1998). Behavioral, neuropsychological, and neuroimaging evidence suggests that
51 these various systems can make differential demands on neural networks of the brain (e.g.,
52 Ashby & Maddox, 2011; Keri, 2003; Nomura & Reber, 2008; Seger & Miller, 2010; Smith &
53 Grossman, 2008). However, describing the algorithm and neural implementation of category-
54 learning systems, as well as the factors that determine when each system will be engaged and
55 how these systems interact, is still a very active endeavor.

56

57 A prominent way to characterize category-learning systems postulates two kinds of
58 categorization processes, rule-based (RB) and information-integration (II), categorization
59 strategies that engage different neurocognitive networks (see Ashby & Maddox, 2011). Within
60 this framework, Maddox, Ashby, and Bohil (2003) have developed a feedback category-learning
61 paradigm with perceptual properties of sine-wave gratings (Gabor patches) that can be varied
62 parametrically to create category distributions that encourage either RB or II approaches to
63 category learning (see Figure 1).

64

65 Insert Figure 1 about here

66

67

68

69 RB tasks are those where the categories can be learned via a reasoning process such as
70 hypothesis testing (Ashby, Alfonso-Reese, Turken, & Waldron, 1998; Ashby, Ell, Valentin, &
71 Casale, 2005). By this account, a participant develops a candidate rule (e.g., category A stimuli
72 have gray bars that are thicker than x ; category B stimuli have gray bars thinner than x) that is
73 tested based on the feedback on each trial. After learning, participants can explicitly describe the
74 rule they use to categorize the stimuli. This RB mechanism would require maintaining and
75 updating the rule, with the boundary condition represented both in working memory, dependent
76 on prefrontal cortex (PFC), and in long-term memory, dependent on medial temporal lobe (MTL);
77 (Nomura & Reber, 2012).

78

79 In contrast, II learning appears to occur implicitly, such that the rule for the category
80 structure is difficult to learn consciously or to describe verbally. II tasks appear to encourage
81 participants to consider the stimuli holistically, integrating perceptual information from different
82 stimulus features early during processing. II learning may depend on implicit learning supported
83 by computations involving the caudate nucleus and visual processing areas in occipital cortex
84 (Nomura & Reber, 2012). Dopaminergic reward circuits of the caudate may be responsible for
85 associating specific categories with neuronal patterns in occipital cortex that code for relevant
86 visual features (Ashby, Alfonso-Reese, Turken, & Waldron, 1998).

87

88 Numerous behavioral experiments comparing RB and II category learning have shown
89 that they are employed using dissociable strategies. For example, working memory dual-task
90 procedures interfered with RB much more than with II learning (e.g., Zeithamova & Maddox,
91 2006; Zeithamova & Maddox, 2007). Delaying feedback beyond an initial period did not
92 interfere with RB learning but disrupted II learning (e.g., Maddox, Ashby, & Bohil, 2003).
Changing the response key associated with a particular category also interfered with II but not

93 RB categorization, suggesting that II learning may require stimulus-response association learning
94 with relatively immediate feedback, characteristics associated with implicit procedural learning
95 (Ashby, Ell, & Waldron, 2003).
96

97 Mechanistically RB processing is thought to depend on hypothesis testing. For instance a
98 participant trying to categorize line segments into two groups might hypothesize that length is
99 what matters, with long segments being one category and short segments being the other. On
100 each trial they test their theory with a response to each line segment. While they may find
101 support for their theory quickly they gradually build a representation of the category threshold
102 that allows them to improve their performance. After each test of their hypothesis they then need
103 to update their memory with whether the test worked and with a candidate threshold value. This
104 evaluation requires selective attention and working memory, likely implemented in PFC, as well
105 as the ability to form enduring mental representations of the rule and boundary condition
106 dependent on the hippocampus and MTL. In contrast, II learning is believed to require
107 integration of multiple stimulus attributes at a predecisional stage (Ashby et al., 1998). Unlike in
108 RB learning, learners frequently cannot articulate what they have learned, but can show their
109 learning through successful performance, a hallmark of nondeclarative memory (Squire, 2009).
110 Thus, II learning may be likened to gaining category expertise with complex objects such as
111 faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996) or Greebles (Rossion, Gauthier,
112 Goffaux, Tarr, & Crommelinck, 2002).
113

114 Working from this distinction, functional magnetic resonance imaging (fMRI) methods
115 have been useful to spatially dissociate categorization when participants learn either an RB or II
116 category distribution. In a study by Nomura and colleagues (2007b), participants who learned
117 the RB distribution showed greater activation in the MTL on correct than incorrect trials, while
118 participants who learned the II distribution showed greater activation in the body of the caudate
119 on correct than incorrect trials. Another category learning study using a different paradigm
120 likewise found activity in the body and tail of the caudate and putamen to be active when
121 learning stimulus-category associations (Cincotta & Seger, 2007). Nomura and Reber (2012)
122 subsequently reanalyzed several sets of RB/II paradigm fMRI data (Nomura, Maddox, & Reber,
123 2007a; Nomura et al., 2007) using PINNACLE (Parallel Interactive Neural Networks Active in
124 Category Learning), a computational model that includes multiple competing categorization
125 systems. Using a participant's behavioral decision data, PINNACLE employs principals of
126 Decision-Bound Modeling Theory (Ashby & Maddox, 1993) to estimate which categorization
127 system is likely engaged on a given trial. Thus, it can be used to sort trials of neuroimaging data
128 to obtain estimates of the neural correlates for individual category-learning systems. This
129 approach identified areas in PFC important for correct decisions during RB category learning, a
130 finding consistent with another previous fMRI study of RB category learning (Filoteo et al.,
131 2005). Posterior regions of occipital cortex were associated with correct decisions during II
132 category learning, a finding consistent with previous fMRI studies of implicit category learning
133 (Reber, Stark, & Squire, 1998a; Reber, Stark, & Squire, 1998b; Waldschmidt & Ashby 2011). In
134 addition, this approach found evidence that regions of dorsolateral PFC were involved in the
135 process of resolving competition between the two systems based on the model-identified
136 moments of high levels of inter-system competition.
137

138 Further progress in understanding the neurocognitive mechanisms of category learning
139 will depend on the ability to measure relevant processing. In particular, measures with high
140 temporal resolution are needed to comprehensively distinguish RB and II mechanisms. In the
141 present study we computed event-related potentials (ERPs) from scalp electroencephalographic
142 (EEG) recordings to examine neural correlates of category learning during both categorization
143 and feedback stages. Participants learned RB and II category distributions during separate
144 testing sessions and their responses were analyzed using Decision-Bound Modeling Theory
145 (Ashby & Maddox, 1993) to identify participants likely to be using RB and II category learning
146 processes with corresponding distributions. Based on prior behavioral and neuroimaging results,
147 we anticipated that RB and II category learning mechanisms would produce different ERPs,
148 when comparing successful (correct) and unsuccessful (incorrect) trials. Specifically, we
149 anticipated differences in an early occipital N1 ERP previously associated with visual category
150 learning (Curran, Tanaka, & Weiskopf, 2002), and consistent with occipital activation found for
151 II category learning in our previous work (Nomura & Reber, 2012). Secondly, given the
152 previously demonstrated reliance of RB category learning on MTL (Nomura et al., 2007b; Seger
153 & Cincotta, 2006; Seger, Dennison, Lopez-Paniagua, Peterson, & Roark, 2011) we predicted that
154 a Late Positive Complex (LPC) ERP associated with explicit memory (Voss & Paller, 2008)
155 would be modulated by accuracy in the RB condition but not the II condition. Lastly, to the
156 extent that RB learning is more explicit than II learning (Huang-Pollock, Maddox, & Karalunas,
157 2011; Seger, Dennison, Lopez-Paniagua, Peterson, & Roark, 2011), we anticipated that the P300
158 to positive feedback would index participant's confidence in their learning (Hajcak, Holroyd,
159 Moser, & Simons, 2005).

160

161 **2. Materials and Methods**

162

163 **2.1 Task Description**

164

165 We used a visual category-learning paradigm (Maddox, Ashby, & Bohil, 2003) in which
166 subjects learned to categorize visual stimuli into two categories via feedback given at the
167 conclusion of each trial. Stimuli were circular sine-wave gratings that varied in spatial frequency
168 (thickness of lines) and spatial orientation (tilt of lines). For the RB distribution, the stimuli were
169 divided into two categories based on a vertical decision boundary such that category membership
170 depended only on the spatial frequency of the sine-wave grating (Figure 1a). For the II group,
171 the categories were defined by a diagonal decision boundary that required integration of
172 frequency and orientation information (Figure 1b). Trial timing was similar to that used by
173 (Nomura et al., 2007b) in their fMRI study (Figure 2).

174

175 Insert Figure 2 about here

176

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178

178 **2.2 Participants**

179

180 Twenty-eight Northwestern University students served as participants in this experiment.
181 Participants received US\$15 per hour for two 2- to 3-hour testing sessions. Participants
182 categorized the RB and II category distributions in separate sessions 1 week apart. Distribution

183 order was counterbalanced across participants. Participants gave informed consent according to
184 the oversight of the Northwestern University Institutional Review Board.

185

186 **2.3 Procedure**

187

188 **Prelearning.** In order to rule out differences in ERPs due to differences in the physical
189 stimuli in the RB and II distributions participants passively viewed 160 sine-wave gratings from
190 both distributions over the course of two blocks prior to attempting to learn categories. Gratings
191 were representative of the range of spatial frequency and orientation used during category
192 learning. Prelearning trial timing was identical to that during category learning, but participants
193 did not make a response during prelearning and did not receive any category information.

194

195 **Category Learning.** Participants categorized 320 sine-wave gratings presented in four
196 blocks during each category-learning session. One session involved the RB distribution and the
197 other session involved the II distribution. Distribution order was counterbalanced across
198 participants. Prior to testing, subjects were familiarized with the procedures, including trial
199 timing, button pressing, and feedback. Participants did not receive instructions about the nature
200 of the categories; rather, they were asked to discover the categories with the aid of auditory
201 feedback. Participants received auditory feedback 2.5 s after stimulus onset. For a correct
202 decision the feedback was a bell sound. For incorrect decisions the feedback was a short buzzer,
203 while participants heard a long buzzer when no response was made in the allotted 2 s. Responses
204 after 2 s were not considered in the analysis. Subjects were debriefed about their categorization
205 strategies after the second testing session.

206

207 **EEG.** Continuous EEG recordings were made during prelearning and category-learning
208 blocks from 59 evenly distributed scalp sites using tin electrodes embedded in an elastic cap
209 (Figure 3). Four additional electrodes were used for monitoring horizontal and vertical eye
210 movements, and two electrodes were placed over the left and right mastoid bones. Participants
211 were instructed to attempt to refrain from blinking or moving their eye position from fixation
212 during the categorization portion of each trial. Electrode impedance was ≤ 5 k. EEG signals
213 were amplified with a band pass of 0.05–200 Hz and sampled at a rate of 1000 Hz. The online
214 reference (left mastoid) was changed to average mastoids offline and a 59- to 60-Hz band-stop
215 filter was applied. EMSE Software Suite (Source Signal Imaging, San Diego, CA) was used to
216 process raw EEG files and to compute ERPs. EOG artifacts were corrected by using a blink-
217 correction algorithm based on independent component analysis. Averaging epochs for stimulus
218 and feedback lasted 1200 ms, including a 200 ms pre-stimulus baseline. Trials showing a greater
219 than 100 μ V deflection during the epoch were discarded. Fewer than 15% of trials were
220 excluded for any given condition for any given participant.

221

222 Insert Figure 3 about here

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225

226 **Decision-Bound Theory Modeling.** Although participants received stimuli drawn from
227 either the RB distribution or from the II distribution within each session, some participants
228 would be expected to fail to adopt the optimal categorization strategy. As in prior work (Ashby
& Maddox, 1993; Nomura & Reber, 2012), we used Decision-Bound Theory (DBT) models to

229 classify behavioral patterns as consistent with either an RB strategy or II strategy. For each
230 participant, the pattern of categorization responses across the stimulus space was compared to an
231 RB-F model based on stimulus spatial frequency (thinness of the black/white strips reflected as a
232 vertical boundary in stimulus space), an RB-O model based on spatial orientation (angle of the
233 black/white strips reflected as a horizontal boundary in stimulus space) and an II model based on
234 a diagonal partition of the stimulus space. The specific placement of the category boundary was
235 optimized to the participant's behavior and the quality of the fit was contrasted across models.
236 By this method, performance in each session can be identified as consistent with either an RB or
237 II approach that either is relatively optimal for the administered stimulus set or reflects a
238 suboptimal strategy. We fit each block of 80 trials using the DBT model. Participants whose
239 performance was consistent with task demands (i.e., at least three of four blocks showed model-
240 to-distribution agreement) were considered the Model-Conforming group and the remaining
241 participants were designated as the Model-Nonconforming group. Using this technique to
242 identify participants most clearly expressing the appropriate strategy strengthens the comparison
243 of ERP differences between RB and II category learning.

244

245 **3. Results**

246

247 All 28 participants exhibited an RB distribution response best fit by an RB-F DBT model.
248 For II, only 15 participants comprised the Model-Conforming Group because they exhibited an II
249 distribution response profile best fit by an II DBT model. In contrast, 13 participants comprised
250 the Model-Nonconforming Group because they exhibited an II distribution response profile best
251 fit by an RB-F or RB-O DBT model (see Figure 4 for distribution profiles from representative
252 participants). Likewise, when the fits for these two groups were compared directly, the first
253 group of participants exhibited better II model fits than did the second [$t(26) = 2.7, p = .01$].
254 However, these two groups did not differ in the quality of their RB model fits with the RD
255 distribution [$t(26) = .02, ns$]. DBT model fitting thus allowed data from participants who were
256 likely using a unidimensional RB strategy with the II category distributions to be excluded from
257 subsequent analyses.

258

259 Insert Figure 4 about here

259

260

261 **3.1 Behavioral Performance**

262

263 Of the 15 participants whose DBT fits were consistent with II strategy use with II
264 distributions, two did not have an adequate number of incorrect trials (< 30) to allow for the
265 correct/incorrect ERP analysis, so their results were excluded from further analysis. Data from
266 one additional participant were eliminated because of poor EEG quality.

267

268 To evaluate potential differences in category-learning accuracy for the RB and II
269 distributions, we ran a 2 (RB vs. II) by 4 (block) repeated-measures ANOVA. Accuracy for RB
270 and II distributions (Figure 5a) did not reliably differ [$F(1,11) = 1.6, p = .23, \eta_p^2 = .13$]. There
271 was a main effect of block [$F(3,33) = 24, p < .001, \eta_p^2 = .69$], and category learning linearly
272 increased over blocks [$F(1,11) = 50, p < .001, \eta_p^2 = .81$]. However, RB and II distributions did
273 not differ with respect to this pattern [$F(1,11) = .4, p = .5, \eta_p^2 = .04$]. Thus, observed differences

274 in correct/incorrect ERP subtractions (described below) cannot easily be attributed to differences
275 in accuracy between RB and II learning.

277 Insert Figure 5 about here

280 Next we looked for potential differences in category-learning RT for the RB and II
281 distributions by using a 2 (RB vs. II) by 2 (Correct vs. Incorrect) by 4 (block) repeated
282 measures ANOVA (see Figure 5b). Participants were faster on correct than incorrect trials [F
283 (1,11) = 27, $p < .001$, $\eta_p^2 = .71$]. There was also a trend towards faster responses on RB trials
284 compared to II trials [F (1,11) = 4.0, $p = .07$, $\eta_p^2 = .27$]. Likewise, there was a trend suggesting
285 an interaction between accuracy and distribution type [F (1,11) = 2.6, $p = .14$, $\eta_p^2 = .19$].
286 Participants were faster on correct trials than on incorrect trials for both RB distributions [F
287 (1,11) = 20, $p < .001$, $\eta_p^2 = .65$] and II distributions [F (1,11) = 14, $p = .003$, $\eta_p^2 = .56$].
288 However, RB and II trials only differed for correct trials [F (1,11) = 6.6, $p = .026$, $\eta_p^2 = .38$] not
289 incorrect trials [F (1,11) = 1.1, $p = .31$, $\eta_p^2 = .09$].

291 3.2 EEG Results

292
293 **Categorization ERPs** Based on our predictions, stimulus-locked analyses were focused
294 on an early occipital N1 ERP (Figure 6) and a later parietal LPC ERP (Figure 7) in the model
295 conforming participants.

297 To measure occipital N1 ERPs, we calculated mean amplitude from 150-250 ms for a
298 cluster of inferior occipital electrodes (Figure 6). The same electrodes and time range were used
299 for every participant. This time range included the occipital N1 peak for all participants. A 2
300 (RB vs. II) by 2 (Correct vs. Incorrect) ANOVA performed on mean amplitudes yielded a
301 reliable interaction between distribution type and accuracy [F (1,11) = 6.1, $p = .03$, $\eta_p^2 = .36$, but
302 no main effect of distribution type [F (1,11) = .05, $p = .8$, $\eta_p^2 = .004$] or accuracy [F (1,11) = .04,
303 $p = .9$, $\eta_p^2 = .003$]. Amplitudes at this latency for correct and incorrect trials were reliably
304 different for the II distribution [F (1,11) = 6.3, $p = .03$, $\eta_p^2 = .37$] and showed a trend in the
305 opposite direction for the RB distribution [F (1,11) = 2.6, $p = .14$, $\eta_p^2 = .19$].

307 Insert Figure 6 about here

309 Also consistent with predictions, we found a stimulus-locked LPC ERP largest over
310 parietal electrodes (Figure 7). To quantify LPC, we measured mean amplitude from 400-700 ms
311 in a cluster of parietal electrodes (Figure 7a). A 2 (RB vs. II) by 2 (Correct vs. Incorrect)
312 ANOVA performed on mean amplitudes yielded a reliable interaction between distribution type
313 and accuracy [F (1,11) = 9.6, $p = .01$, $\eta_p^2 = .47$]. The LPC was reliably larger for correct than
314 incorrect trials in the RB condition [F (1,11) = 20, $p = .001$, $\eta_p^2 = .65$], but not in the II condition
315 [F (1,11) = 3.2, $p = .1$, $\eta_p^2 = .23$]. To uncover relationships between this ERP and performance,
316 we used a smaller parietal region and temporal window (500 – 600 ms) targeted for maximal
317 mean amplitude differences as a function of accuracy. Magnitude of the Correct/Incorrect ERP

318 differences were reliably correlated with RB performance [Figure 6c; $r(11) = .68, p = .01$] but
319 not with II performance [Figure 6e; $r(11) = .05, p = .9$].

320

321 Insert Figure 7 about here

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324

325 **Feedback ERPs** In order to assess hypotheses about the extent to which categorization
326 was based on explicit knowledge, we examined ERPs recorded during feedback (Figure 8).
327 Participants interpret feedback signals as a function of their explicit expectations. P300 responses
328 have been associated with confidence in learning with feedback (Hajcak, Holroyd, Moser, &
329 Simons, 2005). Accordingly, we expected P300 potentials to preferentially index learning in the
330 RB condition, given that implicit learning mechanisms are thought to dominate in the II
331 condition. Both Correct and Incorrect trials showed large positive potentials at approximately
332 300 ms with central-focused topographies (Figure 7b and 7d). A 2 (RB vs. II) by 2 (Correct vs.
333 Incorrect) ANOVA was performed on post-feedback mean amplitudes at 200-400 ms from a
334 cluster of seven central electrodes (Figure 8a). The analysis yielded a main effect of accuracy [$F(1,11) = 43, p < .001, \eta_p^2 = .78$], but no effect of distribution type [$F(1,11) = 0, p = .99, \eta_p^2 = 0$],
335 and no interaction between distribution type and accuracy [$F(1,11) = .25, p = .6, \eta_p^2 = .02$].

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Because P300 is frequently associated with expectancy violations (Polich, 2007) and is
larger when participants receive unexpected feedback (Hajcak, Holroyd, Moser, & Simons,
2005), we hypothesized that participants who were better at RB categorization would show lower
P300 response to correct feedback than would participants who had less-developed rules. To test
this idea, we correlated categorization accuracy with P300 amplitude to correct feedback signals.
Confirming our hypothesis, we found that accuracy was inversely correlated with P300
amplitude for the RB distribution [Figure 8c; $r(11) = -.71, p = .01$], but not for the II distribution
[Figure 8f; $r(11) = .07, p = .83$].

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Because the stimulus-locked LPC during categorization and the feedback-locked P300
both appear to index effective learning in the RB condition, but not in the II condition, we looked
to see whether they were related. The LPC correct/incorrect subtraction is negatively correlated
with the feedback P300 correct/incorrect subtraction in the RB condition ($r = -0.59, p = 0.03$),
but not in the II condition ($r = -0.08, p = .82$). The negative correlation results because the
correct LPC is more positive than the incorrect LPC. When the LPC correct/incorrect subtraction
increases with accuracy, so does the P300 subtraction.

354

354 Insert Figure 8 about here

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Prelearning ERPs Our critical comparisons during category learning were between
correct and incorrect trials within either RB or II distributions, not across the two distributions.
Yet, we took steps to ensure that differences were not due to the nature of the stimuli in the RB
versus II distributions. Accordingly, we analyzed ERPs from prelearning at the same latencies
and scalp locations used in the categorization analyses for N1 and LPC. Neither N1 [$t(10) = 1.0$

362 , $p = .34$.] nor LPC [$t(10) = .11$, $p = .91$] differed between the two distributions, confirming that
363 effects can be ascribing to learning rather than physical stimulus differences.

364

365 **4. Discussion**

366

367 ERP measures differentiated RB and II category-learning processes from each other.
368 During categorization, differences in neural activity were observed in an early, occipital N1 ERP
369 component in the form of differential correct/incorrect activity patterns for RB and II conditions
370 (Figure 6). N1 amplitudes in the II condition were more negative for correct than for incorrect
371 trials, while a trend toward the opposite pattern was observed in the RB condition. At a later
372 latency, LPC amplitudes during RB learning were larger for correct than for incorrect trials,
373 whereas LPC amplitudes during II learning were not modulated by success (Figure 7). In
374 addition, a central P300 ERP to positive feedback was correlated with accuracy for the RB but
375 not the II condition (Figure 8). Together, these differences in brain waves associated with
376 category learning expand on related results from neuropsychological and fMRI studies. In
377 addition, the current findings add neurocognitive information about the temporal order of
378 processing, as discussed further below. Moreover, the lack of ERP differences for stimuli prior
379 to learning makes it possible to rule out trivial physical stimulus factors. Accordingly, we
380 attribute these ERP differences to the distinctive neurocognitive computations engaged during
381 category learning and use.

382

383 RB processing is thought to depend on hypothesis testing, whereby a candidate rule is
384 evaluated by comparing the representation of the stimulus in the current trial to that of a
385 representation of a category threshold. This evaluation requires selective attention and working
386 memory, likely implemented in PFC, as well as the ability to form enduring mental
387 representations of the rule and the threshold, dependent on the hippocampus and MTL. In
388 contrast, II learning may be likened to gaining category expertise with complex objects such as
389 faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996) or Greebles (Rossion, Gauthier,
390 Goffaux, Tarr, & Crommelinck, 2002).

391

392 ERP results were consistent with both of these descriptions. The more positive potential
393 for correct compared to incorrect RB trials late during each trial (Figure 7) is similar to positive
394 potentials that have been found in many different tasks and variously referred to as the P3b,
395 P600, or late-positive complex (LPC). These positive potentials with broad parietal topographies
396 have been associated with working memory (Kok, 2001; Polich, 2007) and episodic memory
397 retrieval (Fernandez et al., 1999; Guillem, Rougier, & Claverie, 1999; Halgren et al., 1994;
398 Paller, Zola-Morgan, Squire, & Hillyard, 1988; Paller, Voss, & Westerberg, 2009). The LPC
399 found here may reflect retrieval/updating of the categorization rule and some mental
400 representation of the boundary condition, two functions consistent with the function of
401 anatomical regions previously associated with the RB category-learning system (Filoteo et al.,
402 2005; Nomura et al., 2007b; Nomura & Reber, 2012; Seger & Cincotta, 2006; Seger, Dennison,
403 Lopez-Paniagua, Peterson, & Roark, 2011). Likewise, we only found these LPC differences
404 when participants' categorization response patterns suggested they are using a simple rule based
405 on a single feature. Similarly, the magnitude of the Correct/Incorrect difference was positively
406 correlated with individual participant categorization success.

407

408 LPC potentials were also apparent in the II condition, but there were no reliable
409 differences between Correct and Incorrect trials, and the magnitude of the Correct/Incorrect
410 difference was unrelated to individual participant categorization success. One possible
411 explanation for the elevation of the LPC here is that the neural machinery responsible for the
412 LPC is engaged during the II condition, just as it is during the RB condition to update
413 information about the hypothesized rule and boundary condition. This interpretation of the LPC
414 is consistent with context-updating theory whereby information from an incoming stimulus
415 results in revision of a maintained mental representation (Donchin, 1981). Given the gradual
416 nature of feedback learning it is likely that participants are updating the mental representation of
417 the boundary condition throughout successful RB learning. In contrast, when participants are
418 relatively confident of the rule they are using, but uncertain about whether a given stimulus is an
419 A or B they may not update (lower LPC). In the II condition they are constantly trying to update
420 their rule and/or boundary condition, but this does not result in successful learning. In this
421 interpretation the neural systems responsible for the LPC is engaged during II learning, but it's
422 output is likely inhibited (Ashby & Maddox, 2011) and thus not responsible for the final
423 behavioral decisions. Nomura and Reber (2012) proposed that RB and II systems are both
424 active and interact competitively during categorization with the DLPFC resolving this
425 competition based on appraising confidence in both systems. Our LPC ERP is consistent with
426 this proposal that the explicit category-learning system is engaged in both the RB and II tasks,
427 but it is only effective in guiding optimal categorization performance in the RB condition.
428

429 We also observed an early occipital Correct/Incorrect difference wave (Figure 6). A prior
430 visual category learning study also revealed differential effects in the N1 ERP (Curran, Tanaka,
431 & Weiskopf, 2002). The authors speculated that this ERP could be related to the N170 ERP
432 frequently seen in studies of face processing (e.g., Bentin, Allison, Puce, Perez, & McCarthy,
433 1996) and expert categorization (e.g., Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002;
434 Tanaka & Curran, 2001). This type of processing frequently engages extrastriate visual cortex
435 (e.g., Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Kanwisher, McDermott, & Chun,
436 1997), an area found to be more active in the II condition of this task (Nomura & Reber, 2012)
437 and previously implicated in several other category-learning tasks (Reber, Stark, & Squire,
438 1998a; Reber, Stark, & Squire, 1998b). The early time-course of our effect suggests a shaping
439 of visual perception that occurs as part of the category learning process in tasks like II
440 categorization.
441

442 One hypothesis is that the observed N1 may reflect the degree to which a participant uses
443 holistic processing to process the sine-wave gratings. Ashby and Maddox (2011) have argued
444 that II tasks encourage participants to integrate perceptual information from different stimulus
445 features at a predecisional level. In contrast, RB tasks encourage participants to consider single
446 features and judge them against a rule¹. Thus, holistic processing is advantageous with the II
447 distribution, while it may be detrimental with the RB distribution where attention to spatial
448 orientation could distract the participant from focusing on the spatial frequency information
449 necessary to appraise the rule used to define the RB categories in this study. The presence of the
450 N1 effect in both RB and II conditions is also consistent with the idea that both processes are

¹ Or to use a conjunctive rule whereby information about more than one feature is evaluated against a more complex rule at a later stage of processing.

451 regularly active during categorization, but that the results of the earlier II process may be
452 inhibited to allow the RB to respond (Ashby & Maddox, 2011).

453
454 The electrophysiological methods used in this study also allowed us to separate neural
455 correlates of categorization accuracy from neural signals accompanying feedback. We observed
456 a differential Correct/Incorrect P300 response during feedback that did not differ in amplitude
457 between RB and II conditions (Figure 8). However, feedback-related P300 amplitude on correct
458 trials negatively correlated with RB accuracy but not with II accuracy (Figure 8c & f). P300
459 responses to feedback may be sensitive to expectancies, as in prior studies with very different
460 tasks (e.g., Courchesne, Hillyard, & Courchesne, 1977; Duncan-Johnson & Donchin, 1977;
461 Johnson & Donchin, 1980), and when participants receive unexpected feedback (Hajcak,
462 Holroyd, Moser, & Simons, 2005). In the present case, the observed correlations may reflect an
463 explicit/implicit distinction between RB and II category-learning strategies. Specifically, over
464 trials participants in the RB condition are developing a hypothesized categorization rule
465 including a representation for the boundary condition for that rule. Each new stimulus is
466 considered with respect to this context. When those expectations are confirmed by positive
467 feedback, participants are less surprised the more confident they are in their rule and boundary
468 condition representation. In contrast, while participants perform similarly with respect to
469 accuracy in the II condition, they do not become confident in their rule because an explicit RB
470 rule is not driving their performance. This result is consistent with participants' self-reports,
471 which indicate confidence in their rule description after RB learning and little to no confidence
472 after II learning. Thus, these results provide further evidence for an explicit/implicit distinction
473 between RB and II learning.

474
475 The majority of our ERP analyses in this study are based on correct/incorrect subtractions
476 that seek to isolate what is unique about successful RB and II categorization. The advantage of
477 this subtractive approach (see also Normura et al., 2007b) is that aspects of the two tasks that
478 may be common such as seeing the stimulus, making a response, and hearing feedback are
479 subtracted away leaving us with what is unique. However, this means by definition that our
480 descriptions of RB and II category learning are incomplete because these common processes are
481 certainly part of the whole mechanism and may be important to achieve a full understanding of
482 category learning. Likewise, it is difficult for us to use this approach to look at how the
483 category-learning processes changes over time as so does the balance of correct and incorrect
484 trials. Given successful learning, correct trials are more abundant at the end of the experiment
485 than at the beginning when their neural correlates are likely more affected by guessing with
486 either RB or II distributions. These factors are both important, particularly when we consider
487 categories that may be learned and used frequently over the course of a lifetime. Recently, in
488 their ambitious study of expertise in category learning (participants performed ten thousand trials
489 over the course of the experiment compared to our 320 trials), Waldschmidt and Ashby (2011)
490 demonstrated that even when considering just a single distribution type the neural correlates
491 responsible for category use can change as participants approach expertise in categorization.

492
493 In summary, the present ERP findings illustrate two distinct neurocognitive processes
494 responsible for successful category learning. These processes appear to compete on each
495 categorization trial. The II process utilizes a network including, but not limited to the occipital
496 cortex likely reflecting changes in perceptual processing as a result of implicit category learning.

497 In contrast the more deliberative RB process occurs later during processing of a stimulus and
498 employs more anterior cortical regions associated with working and long-term memory, most
499 likely in association with MTL networks. In addition, neural activity measured during feedback
500 suggest participants are aware of their learning when using an RB process to make their
501 categorization decisions, but not when they are using the II process. Our findings do not appear
502 to arise from differences in stimuli, but rather stem from differences in the neurocognitive
503 processes which can be engaged while learning different types of categories. This experimental
504 approach provides new perspectives on these category-learning mechanisms as well as a new
505 way to investigate their interaction and competition during learning.
506

507 **Human Research Statement**

508 Humans participated in this experiment according to procedures approved by the
509 Northwestern University Institutional Review Board. Before beginning the experiment,
510 participants were required to read and sign the informed consent form. They were encouraged to
511 ask any questions and had the option of leaving at any time with no adverse consequences. The
512 informed consent forms are kept on record in the lab.
513

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525 Science Society, Amsterdam, Netherlands, and the 2009 Cognitive Neuroscience Society annual
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Figure Legends

Figure 1. RB and II category distributions used in the study. Sine-wave gratings varied based on spatial frequency and spatial orientation. **(A)** The RB category was defined based on frequency whereas orientation varied unsystematically. **(B)** The II category was defined based on both frequency and orientation with a diagonal decision bound.

Figure 2. Schematic of a single trial. A fixation cross was followed by the to-be-categorized-stimulus for a fixed duration, followed by a short visual mask, followed by auditory feedback and a brief ISI before the next trial. The subject responded “category A” or “category B” during the 2 s the stimulus was on the screen by pressing one of two buttons on a hand-held response box. EEG was recorded continuously, and stimulus- and feedback-locked ERPs were calculated from each trial.

Figure 3. **(A)** Placement of 52 scalp electrodes (of 58 total) used in this study with respect to 10-20 landmarks. **(B)** Frontal (F), Central (C), Parietal (P), and Occipital (O) electrode clusters used for the analysis of the N1. **(C)** Parietal electrode cluster surrounding location Pz used in the analysis of the LPC. **(D)** Central electrode cluster surrounding and including electrode Cz used in the analysis of the feedback P300.

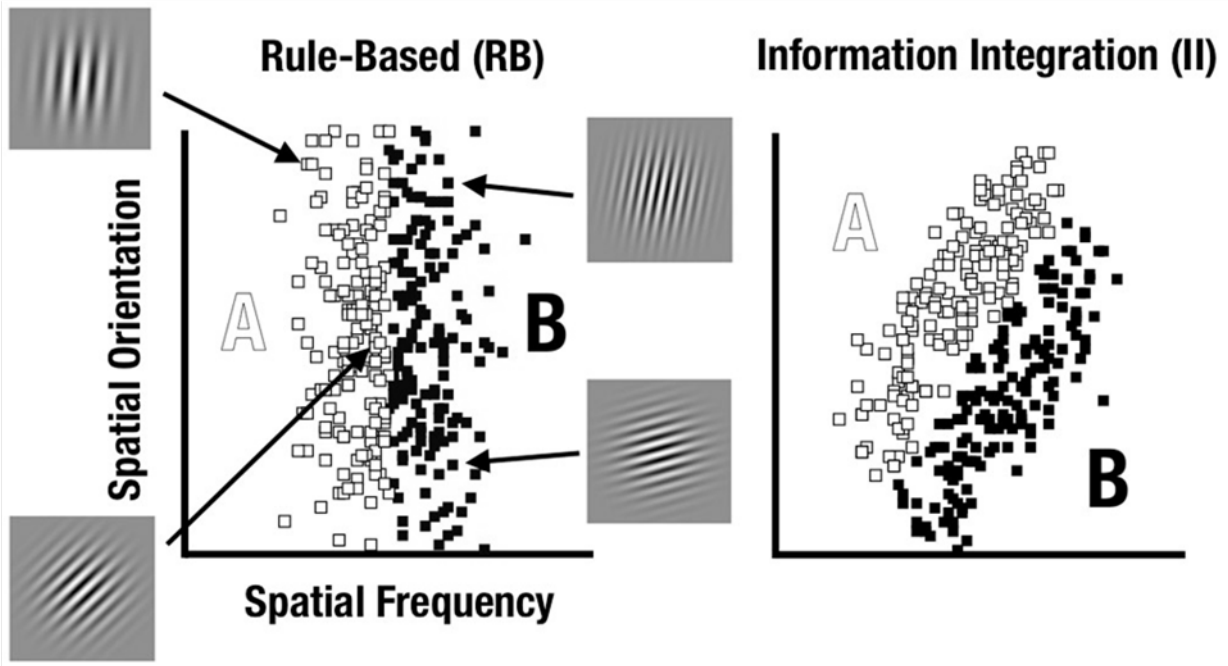
Figure 4. **(A)** II distribution used in the experiment. **(B)** II distribution category responses from a participant whose responses were best fit by a RB DBT model and who was excluded from further analysis. **(C)** II distribution category responses from a participant whose responses were best fit by an II DBT model and who was kept for further analysis.

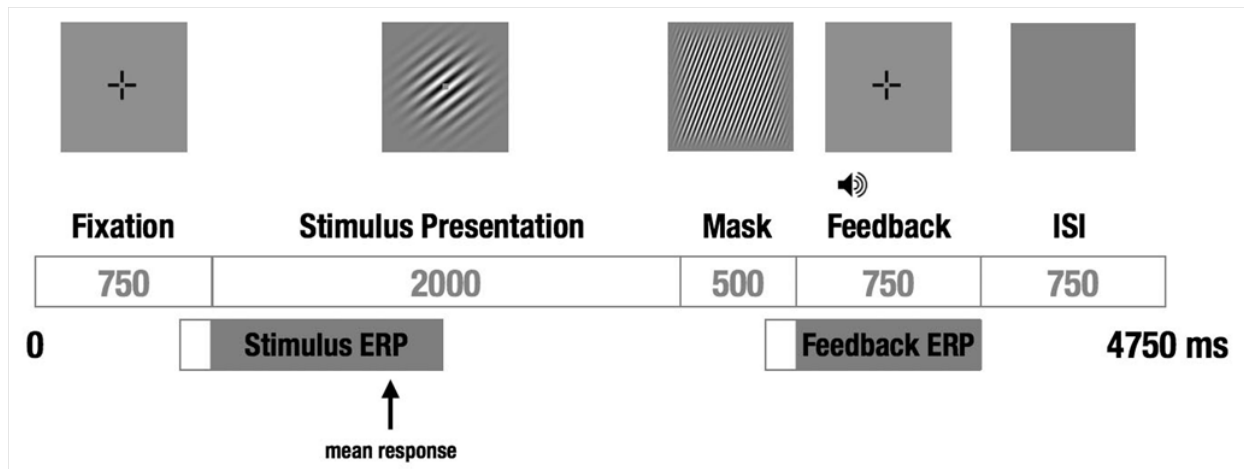
Figure 5. Behavioral results for Model-Conforming Participants. **(A)** Accuracy and **(B)** RTs for participants included based on DBT model fits and included in the analysis of brain potentials. Error bars represent ± 1 standard error of the mean.

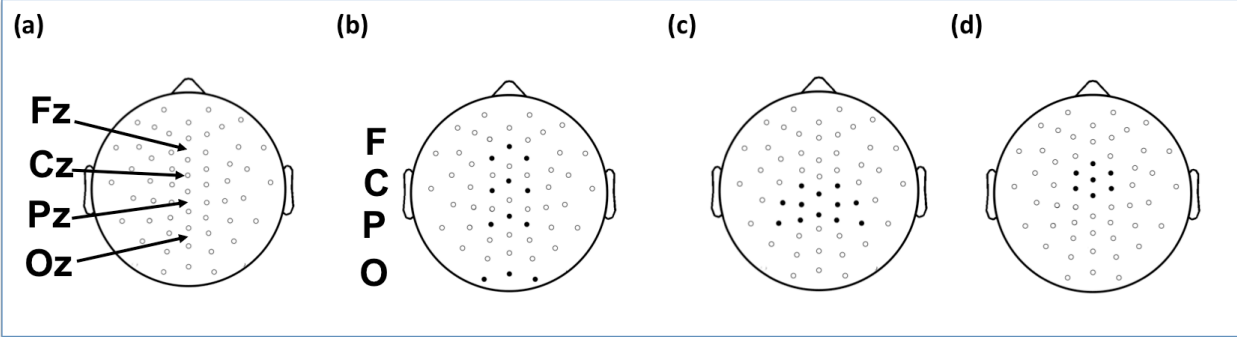
Figure 6. Early stimulus-locked ERPs from frontal (F; three marked electrodes just posterior to Fz), central (C; three marked electrodes including Cz), parietal (P; three marked electrodes just posterior to Pz) and occipital (three marked electrodes just posterior to Oz including the Inion) electrode clusters for **(A)** RB and **(B)** II category-learning conditions.

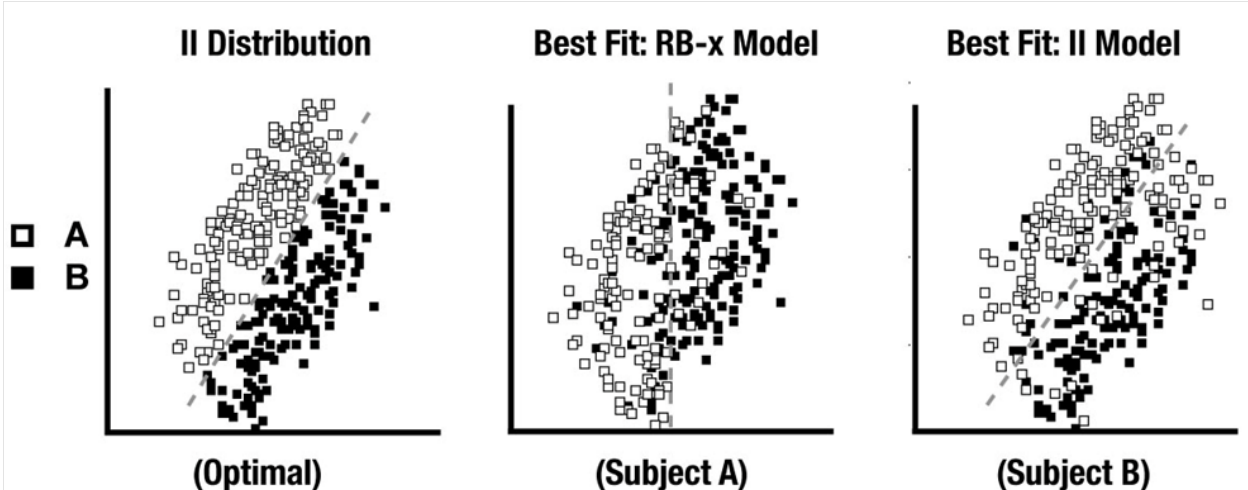
Figure 7. ERPs showing the LPC ERP for both **(A)** RB and **(D)** II conditions in a cluster of parietal electrodes (twelve marked electrodes surrounding Pz). Topographic maps representing correct minus incorrect subtractions from 500 to 600 ms for **(B)** RB and **(E)** II ERPs. Scatterplots showing the relationship of accuracy to the correct minus incorrect mean amplitude ERP subtractions from 500 to 600 ms for three parietal electrodes near Pz (indicated on the corresponding topographic maps) for **(C)** RB and **(F)** II conditions.

Figure 8. Feedback-locked ERPs from a central cluster of electrodes (seven marked electrodes surrounding Cz) for **(A)** RB and **(D)** II category-learning conditions. Topographic maps representing mean amplitude from correct responses from 200 to 400 ms for **(B)** RB and **(E)** II ERPs. Scatterplots showing the relationship of accuracy to mean amplitude for correct trials for **(C)** RB and **(F)** II conditions.

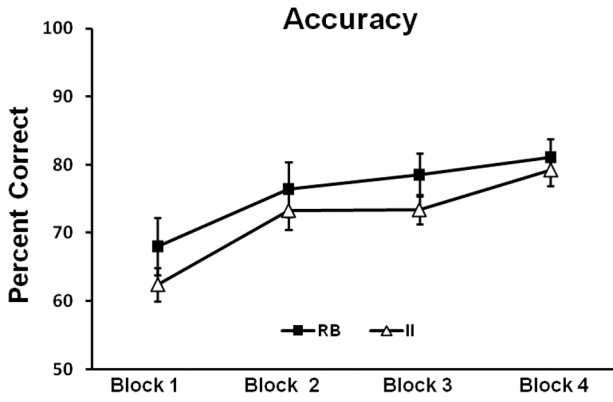




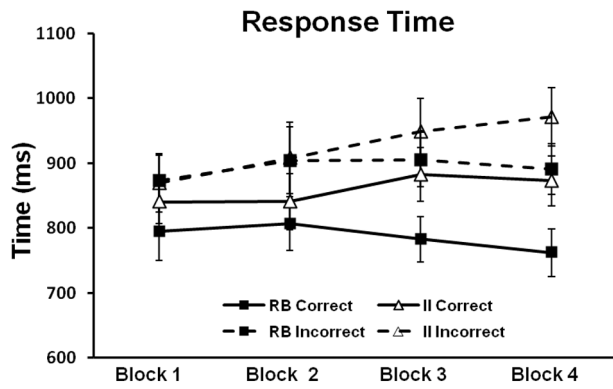




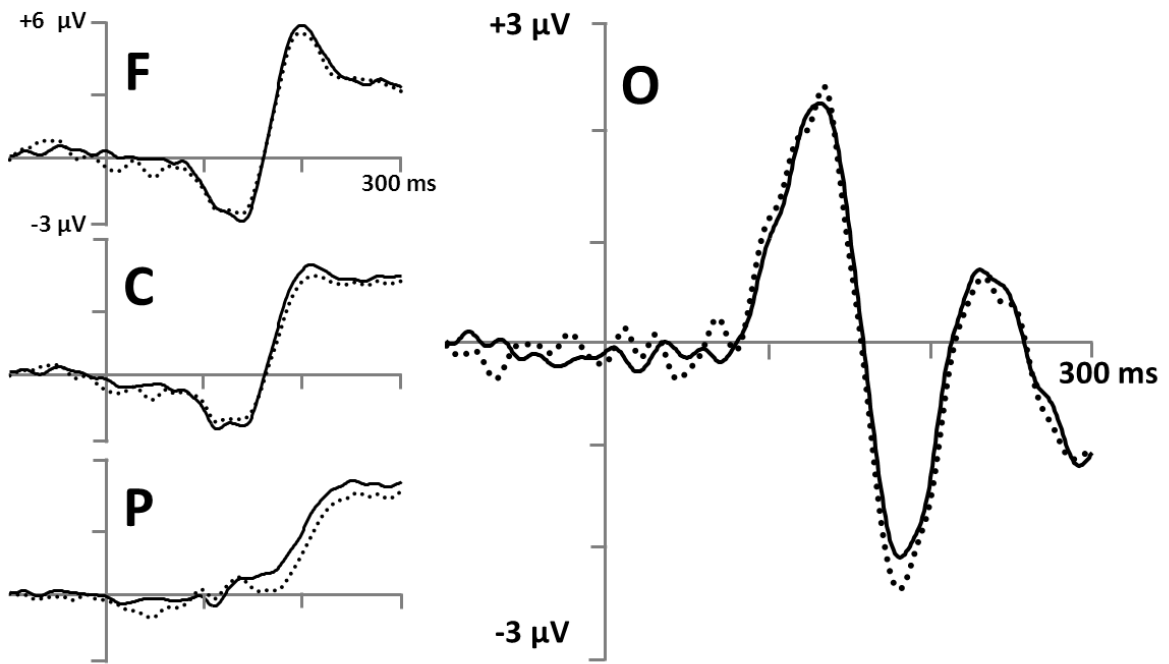
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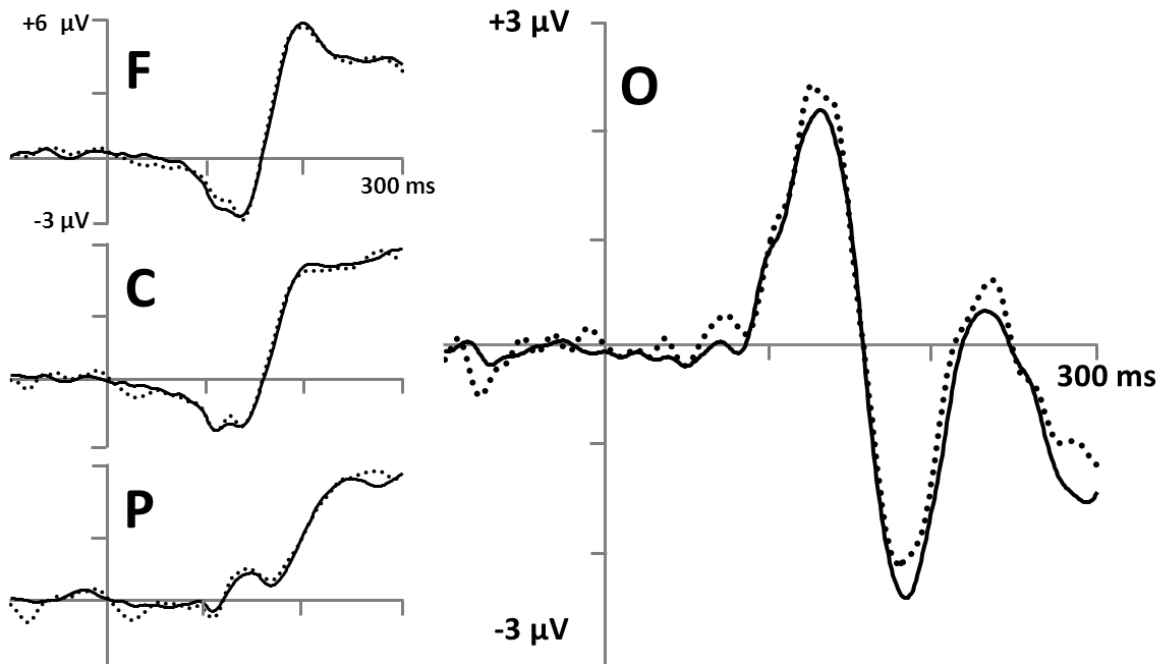
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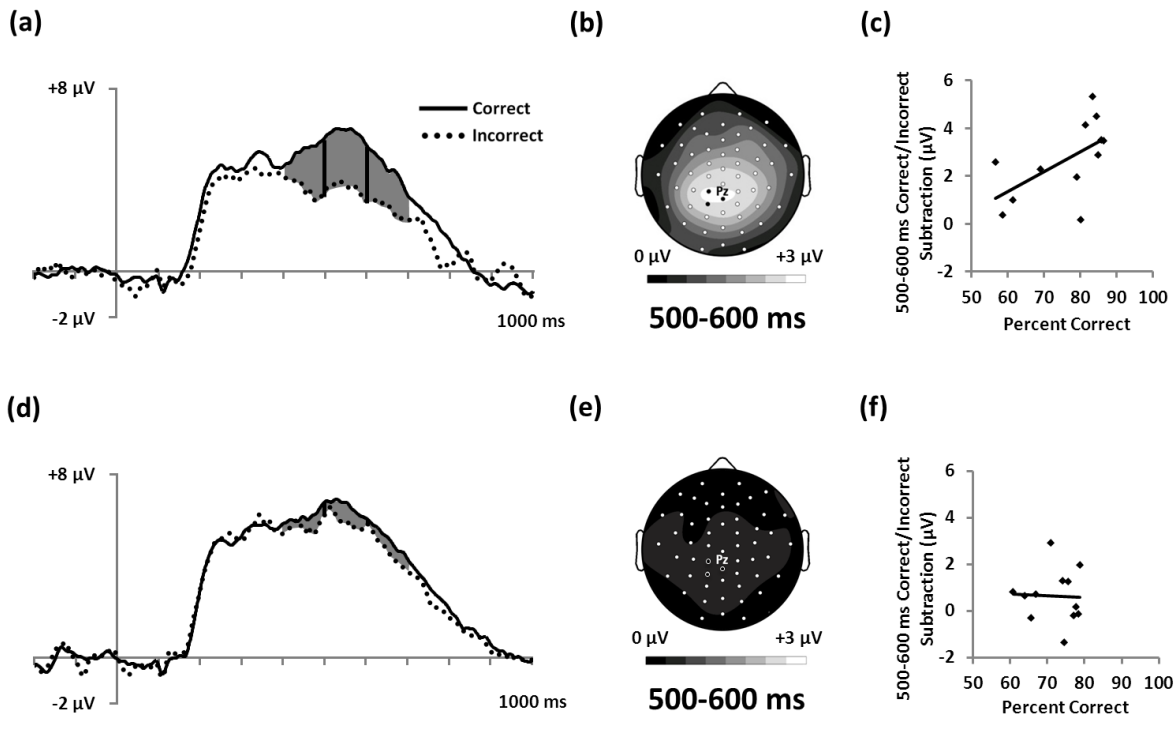


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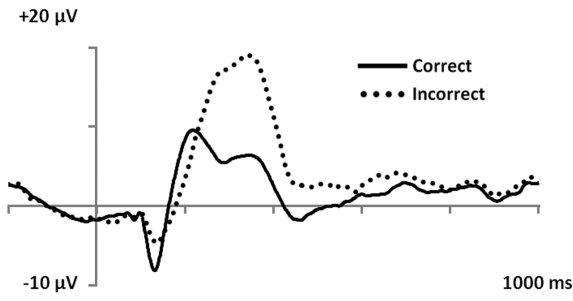


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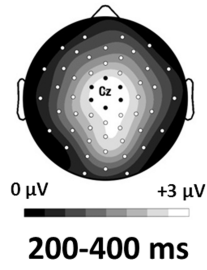




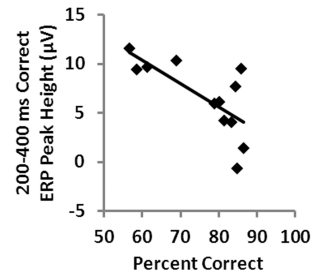
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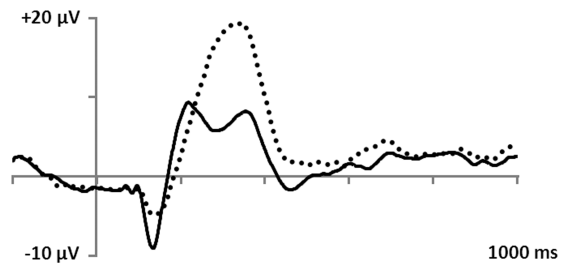
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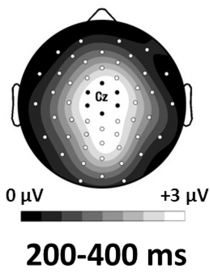
(e)



(d)



(e)



(f)

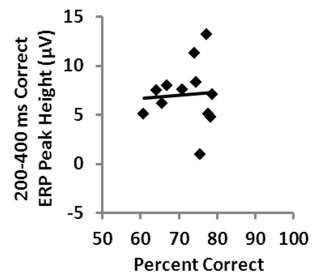


Figure 1.TIF

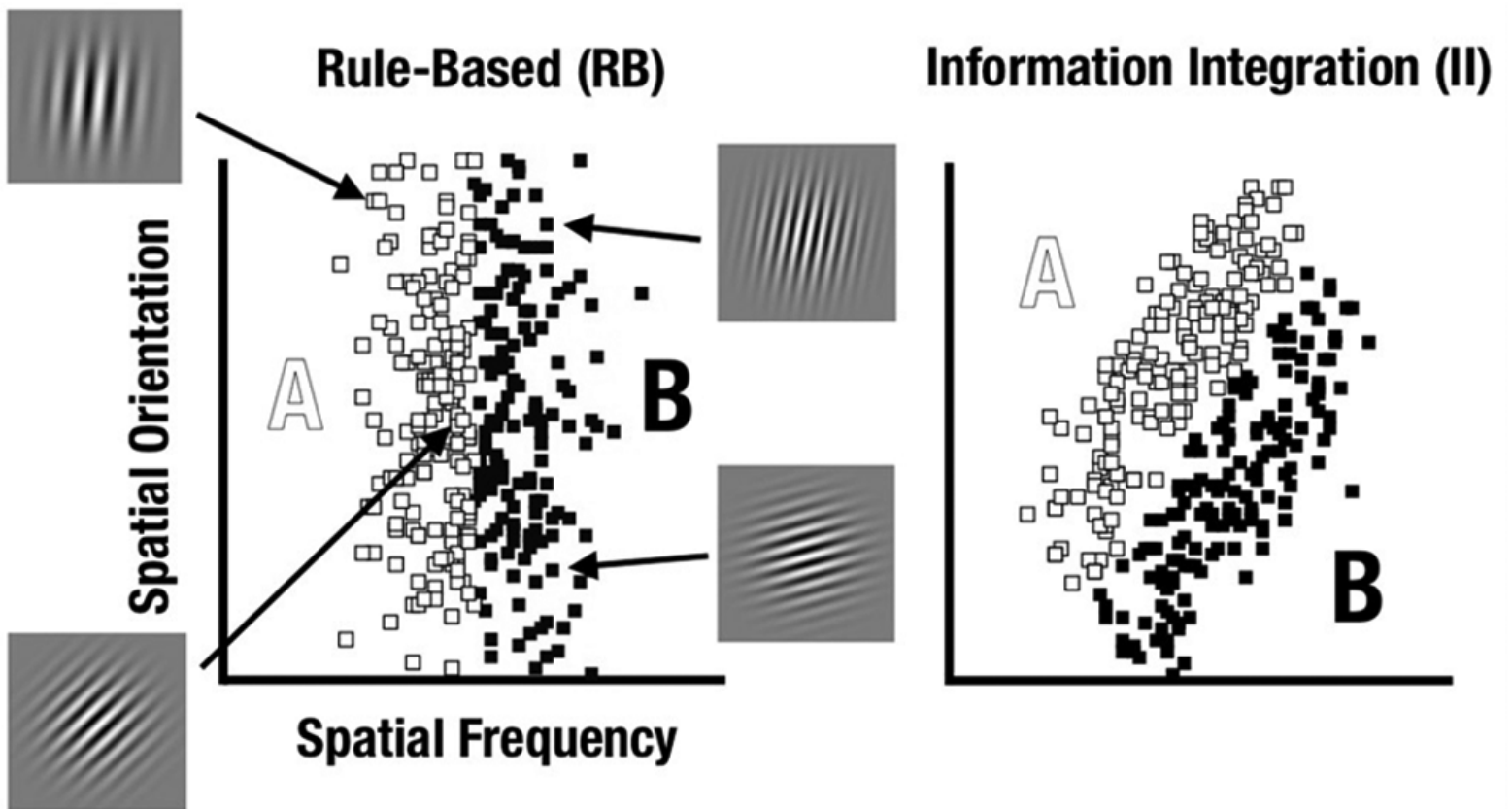
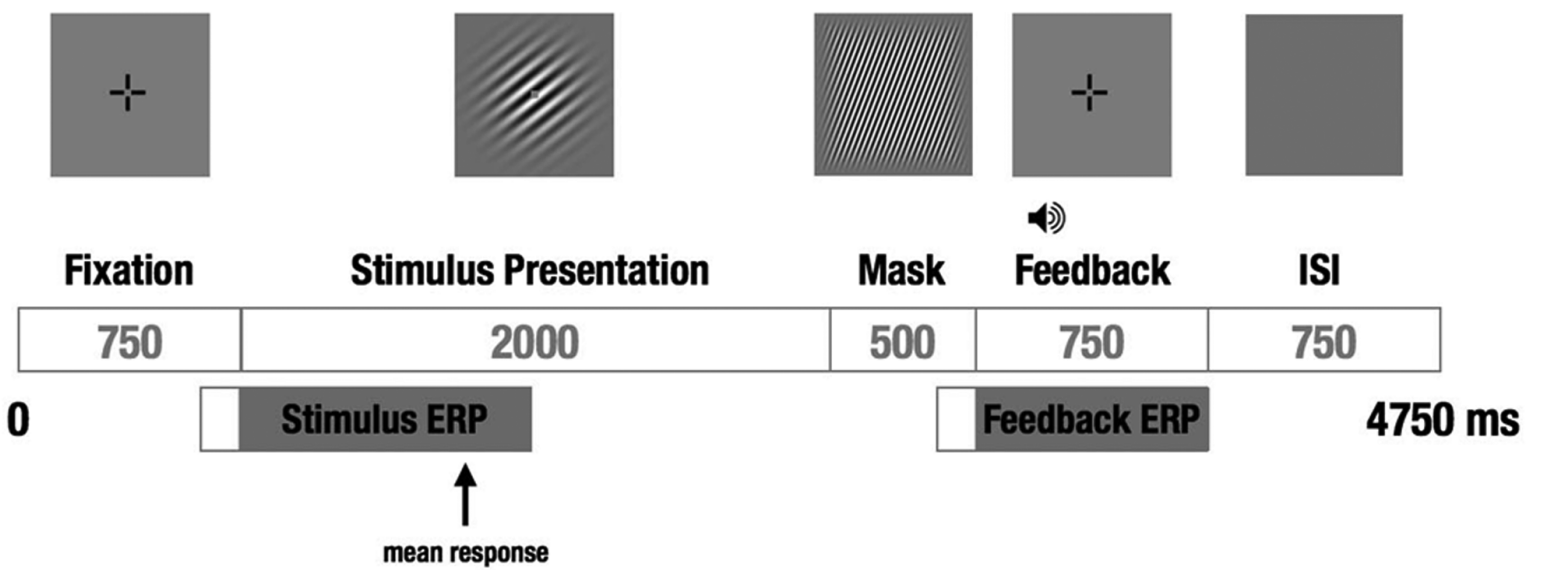
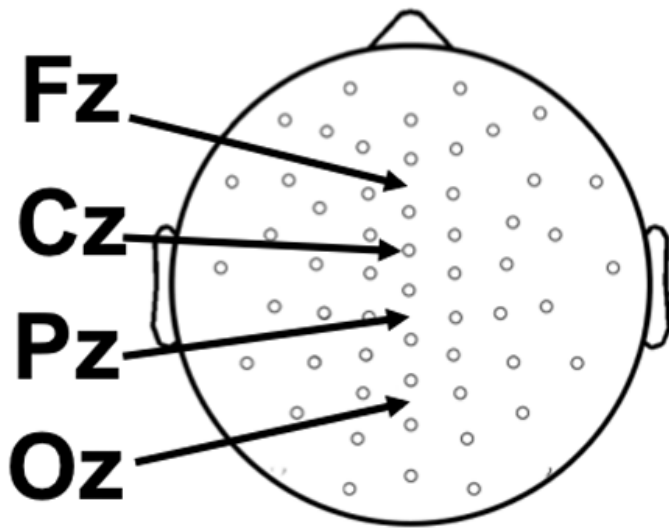


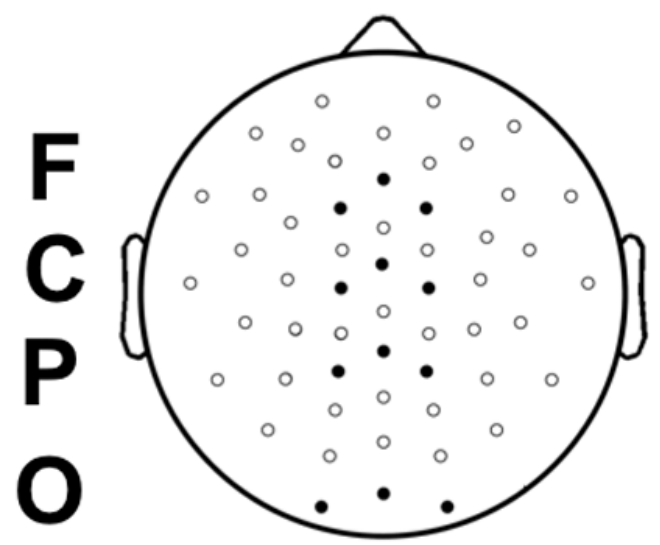
Figure 2.TIF



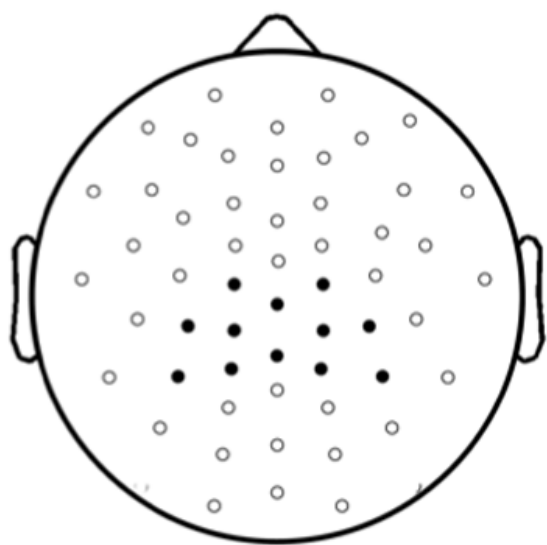
(a)



(b)



(c)



(d)

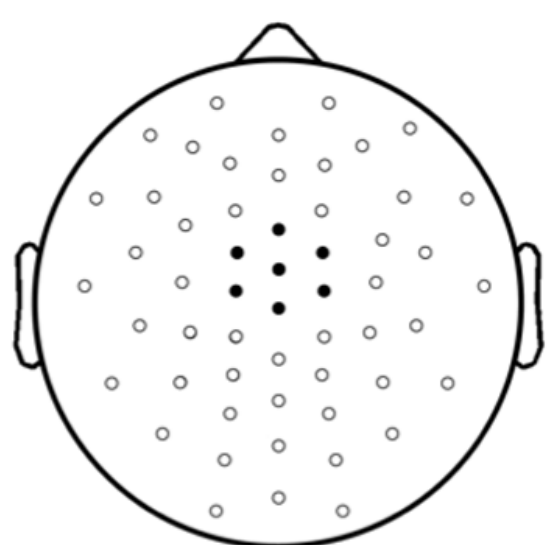


Figure 4.TIF

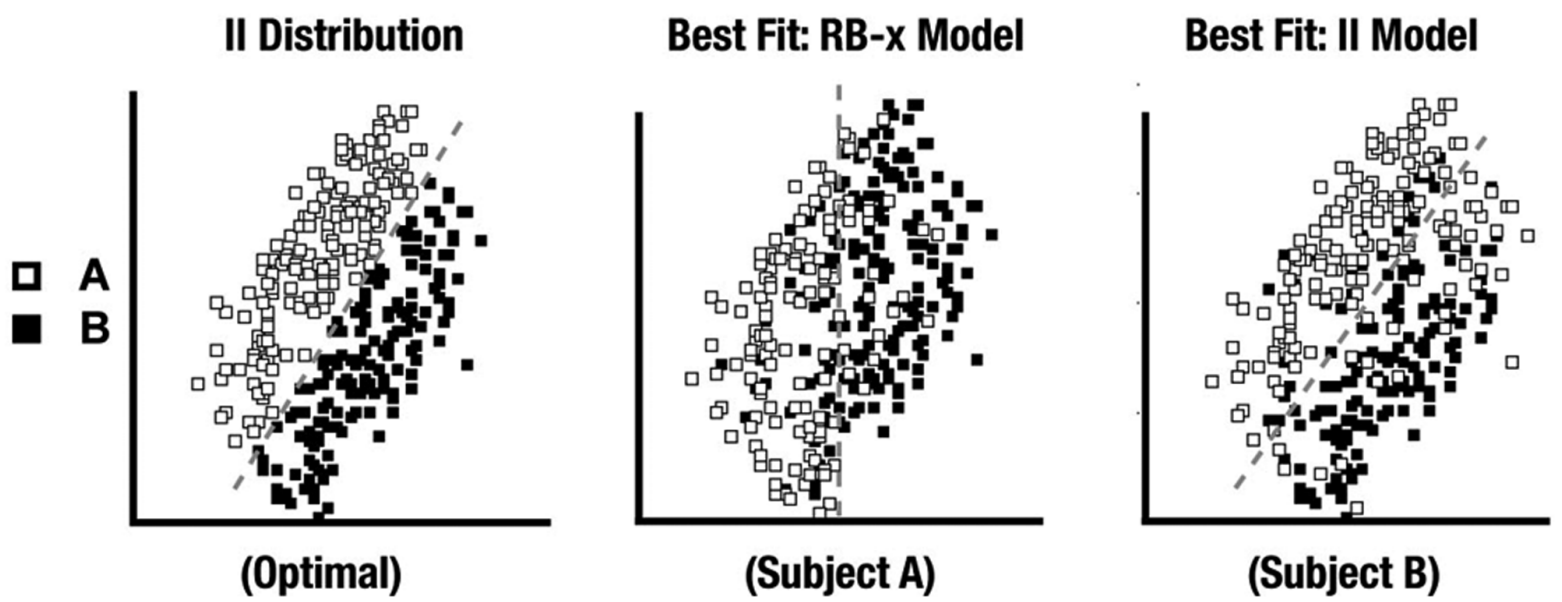
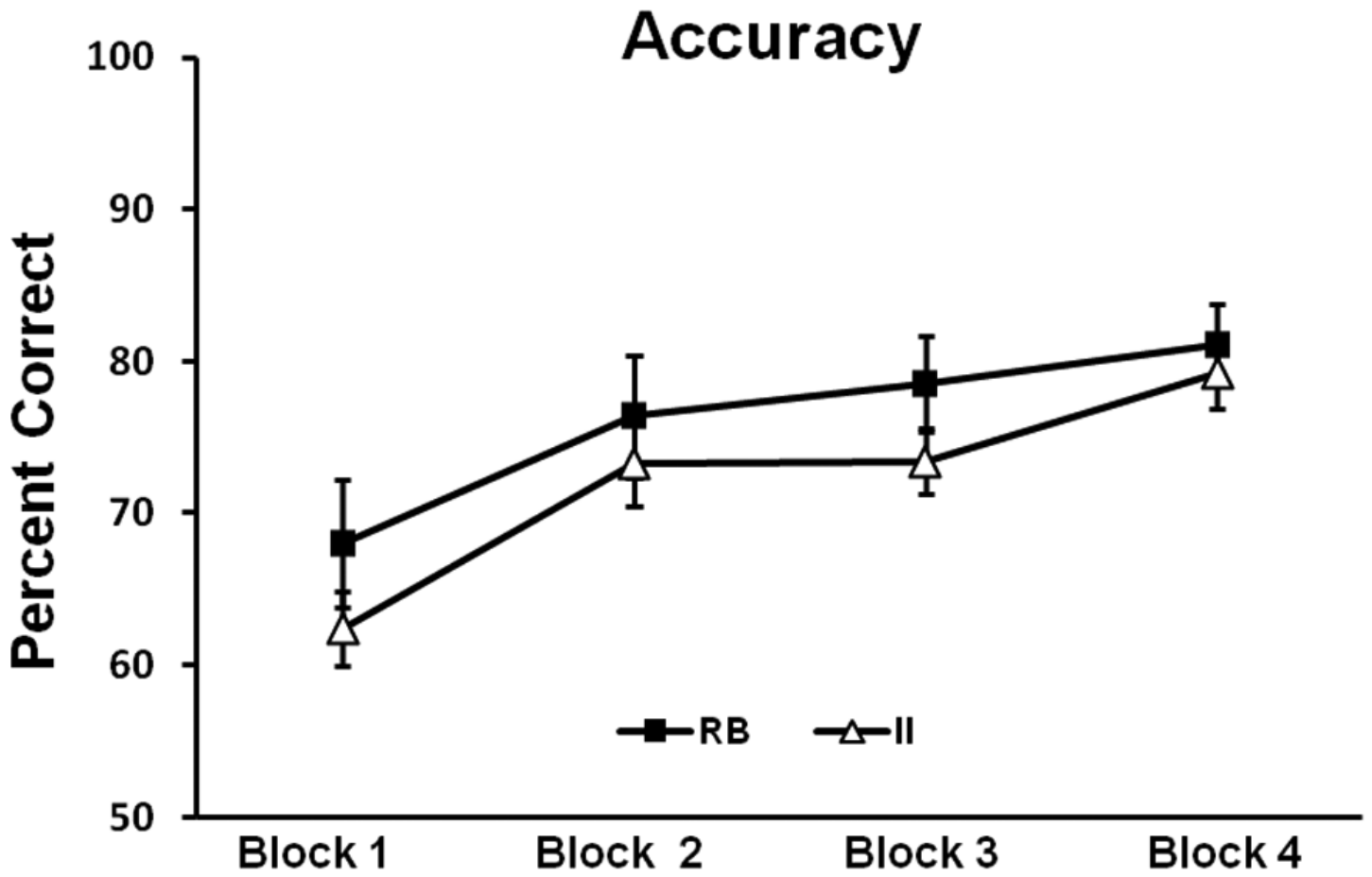


Figure 5.TIF

(a)



(b)

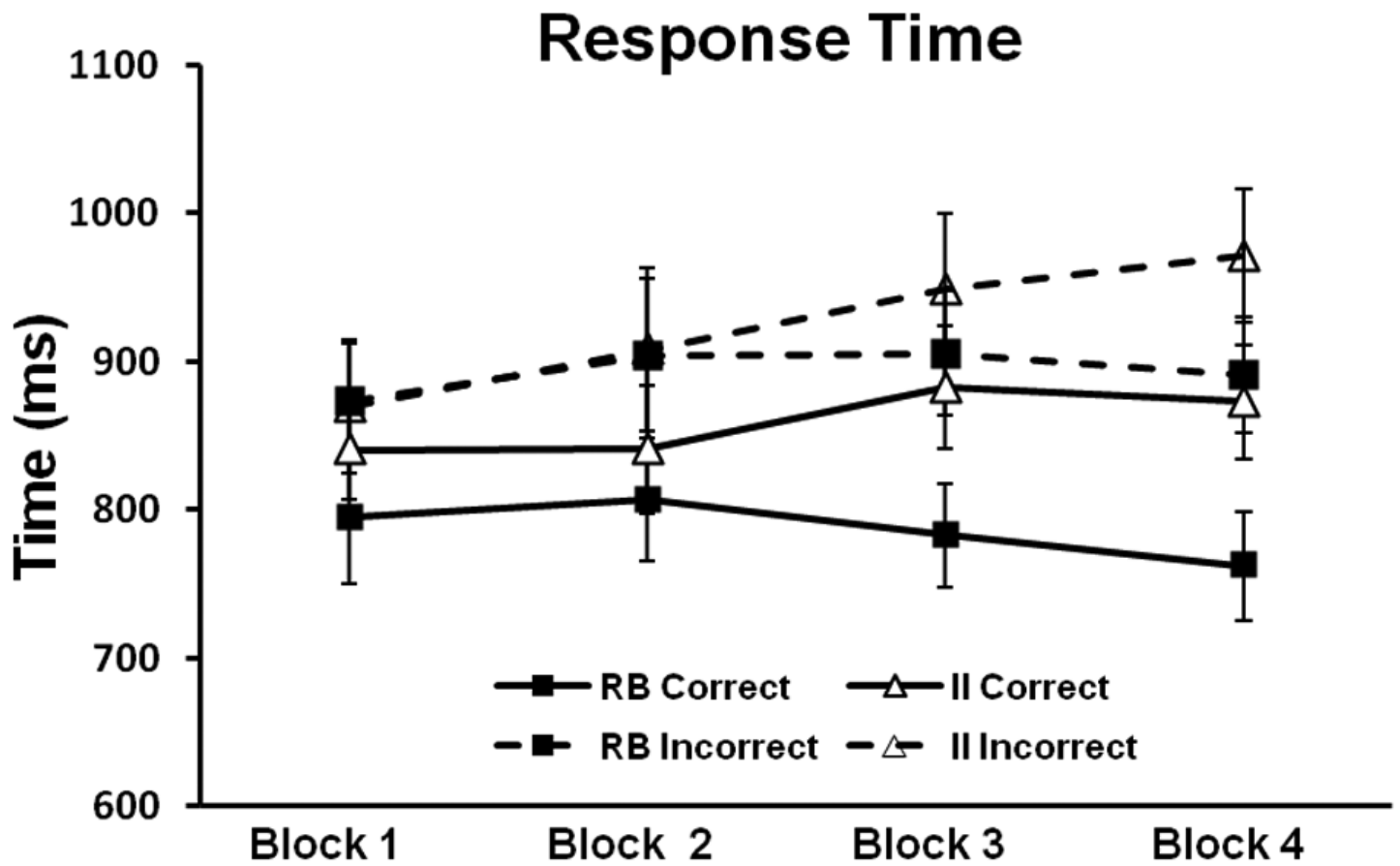


Figure 6.TIF

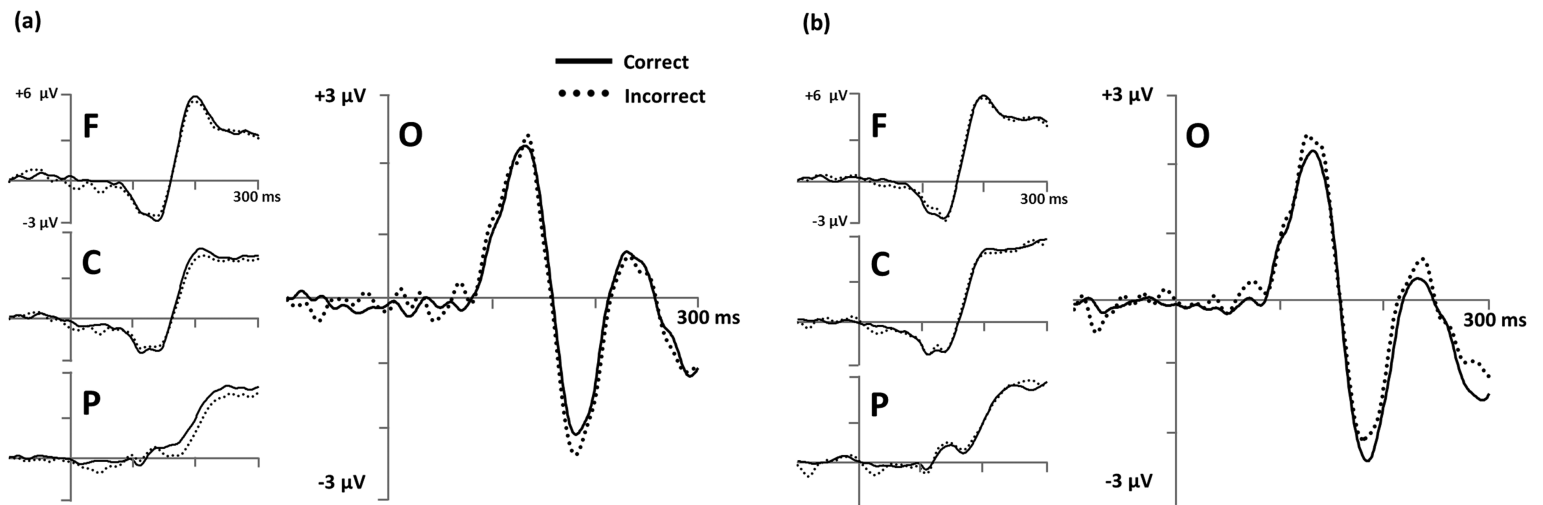
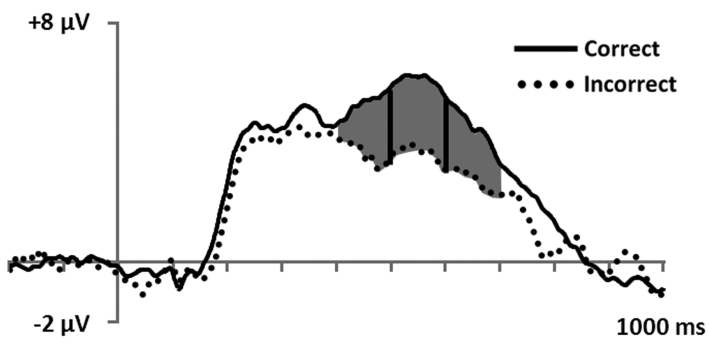
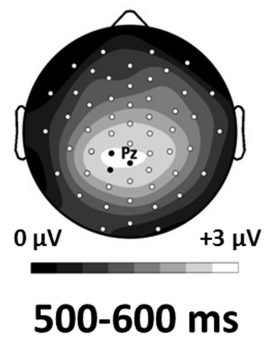


Figure 7.TIF

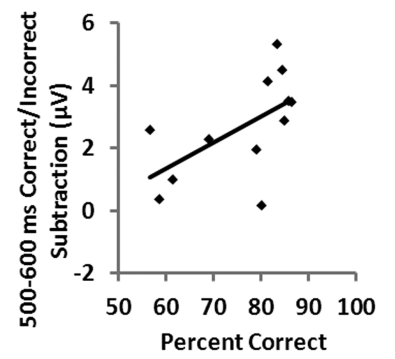
(a)



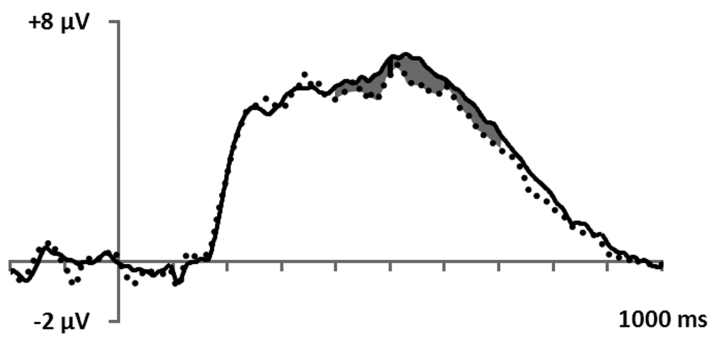
(b)



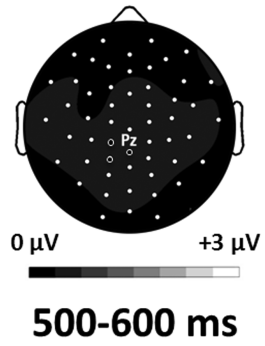
(c)



(d)



(e)



(f)

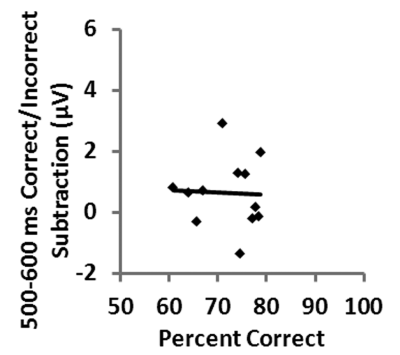


Figure 8.TIF

