

1 **Neural correlates of minimal recognizable configurations in the human brain**

2

3 Antonino Casile¹⁺, Aurelie Cordier²⁺, Jiye G. Kim², Andrea Cometa³, Joseph R. Madsen², Scellig
4 Stone², Guy Ben-Yosef⁴, Shimon Ullman^{4,6}, William Anderson⁵, Gabriel Kreiman^{2,6,*}

5

6 ¹ Department of Biomedical and Dental Sciences and Morphofunctional Imaging
7 University of Messina 98124 Messina (ME), Italy

8 ² Children's Hospital, Harvard Medical School, Boston, MA 02115, USA

9 ³ MoMiLab, IMT School for Advanced Studies, 55100 Lucca (LU), Italy

10 ⁴ Weizmann Institute, Rehovot, Israel

11 ⁵ Department of Neurosurgery, Johns Hopkins Medical School, Baltimore 21205, MD, USA

12 ⁶ Center for Brains, Minds and Machines, Cambridge, MA 02142, USA

13

14 ⁺ Equal contribution

15 ^{*} To whom correspondence should be addressed: Gabriel.kreiman@tch.harvard.edu

16

17

18 **Summary**

19 Inferring object identity from incomplete information is a ubiquitous challenge for the visual system. Here
20 we study the neural mechanisms underlying processing of minimally recognizable configurations (MIRCs)
21 and their subparts which are unrecognizable (sub-MIRCs). MIRCs and sub-MIRCs are very similar at the
22 pixel level, yet they lead to a dramatic gap in recognition performance. To evaluate how the brain processes
23 such images, we invasively record human neurophysiological responses. Correct identification of MIRCs
24 is associated with a dynamic interplay of feedback and feedforward mechanisms between frontal and
25 temporal areas. Interpretation of sub-MIRC images improves dramatically after exposure to the
26 corresponding full objects. This rapid and unsupervised learning is accompanied by changes in neural
27 responses in the temporal cortex. These results are at odds with purely feedforward models of object
28 recognition and suggest a role for the frontal lobe in providing top-down signals related to object identity
29 in difficult visual tasks.

30

31

32

* Lead contact

33 **Introduction**

34 Visual object recognition is robust to an extensive range of image transformations that produce
35 different retinal projections of the same stimulus ^{1,2}. For example, we can easily recognize an object when
36 presented under a wide range of positions, scales, or viewpoints ^{3,4}. A particularly striking example of the
37 robustness of visual perception is the ability to recognize an object when only a fragment of it is shown.
38 Fragmented object views are ubiquitous during natural vision due to occlusion or poor illumination. In these
39 cases, the visual representation of the objects is incomplete, and yet our visual system can quickly, and
40 seemingly effortlessly, compensate for the missing information ⁵⁻¹¹.

41 It has been proposed that objects in the visual scene have features that can be reliably extracted
42 across a wide variety of viewing conditions and which support perception ^{2,12-15}. Several experimental
43 methods that allow the identification of such informative features have been proposed. For example,
44 Gosselin & Schyns (2001) proposed a technique called Bubbles that consisted in presenting objects through
45 apertures to identify specific “critical features” that can aid recognition ¹⁷⁻¹⁹ and are represented in neural
46 signals ^{20,21}. Other studies have used images with different levels of fragmentation or occlusion ^{10,22} to
47 investigate frequency bands or time points of the event-related potentials that are enhanced during
48 recognition ²³⁻²⁵.

49 Recently, Ullman and colleagues extended the notion of critical features in a study that combined
50 large-scale human psychophysical experiments and computer vision ²⁶. By sequentially cropping and
51 blurring images of objects and assessing their recognition rates, the authors identified MInimally-
52 Recognizable Configurations (MIRCs). MIRCs consist of image fragments recognized by human
53 participants but rendered unrecognizable upon the introduction of minimal changes (**Figure 1**). Small
54 reductions of a MIRC image along the horizontal and vertical dimensions lead to a sub-MIRC image with
55 recognition rates that drop by many tens of percentage points ²⁶. This dramatic drop in recognition
56 performance from MIRCs to sub-MIRCs cannot be accounted for by state-of-the-art computer vision
57 models ²⁶ and highlights a critical difference between biological vision and current computational models
58 of vision ²⁷.

59 Occlusion removes large parts of an object from view, but often has a limited impact on perceptual
60 recognition. In contrast, MIRC and sub-MIRC images are very similar in pixel space, but they produce
61 dramatically different recognition performance. Thus, MIRC images offer a unique opportunity to probe
62 visual recognition processes in the presence of stimuli that are very similar at the retinal level while eliciting
63 dramatic differences at the perceptual level ²⁸. To understand the neural mechanisms that lead to recognition
64 of objects from fragments, we set out to investigate the neurophysiological responses in the human brain

65 while participants identified MIRC and sub-MIRC images. We recorded invasive neurophysiological
66 responses from patients with epilepsy implanted with electrodes for clinical purposes and investigated the
67 neural correlates of object recognition by comparing neural responses recorded during recognized MIRCs
68 vs. unrecognized sub-MIRCs images. Furthermore, participants rapidly learned to recognize sub-MIRC
69 images after exposure to the full object images. Such learning was accompanied by neural changes that
70 distinguished between identical images when they were recognized versus when they were not recognized.

71 72 **Results**

73 We recorded intracranial field potentials (IFPs) from 1,752 electrodes (**Table S1, Figures S1 and**
74 **S7**) in 12 participants (5 male, 11–43 years old, **Table S2**) implanted with subdural or deep intracerebral
75 electrodes to localize their epileptic seizure foci. Participants viewed grayscale images for 1s and were then
76 asked to identify them verbally (**Figure 1A**). Participants were given no feedback about the correctness of
77 their responses.

78

79 **Participants rapidly learned to recognize images in an unsupervised fashion**

80 Visual stimuli were a subset of the images used by Ullman and colleagues in a previous large-scale
81 behavioral study ²⁶. The stimuli included images from 10 object categories (**Figure 1B**) or degraded
82 versions of those images obtained by iteratively cropping or changing the resolution of the original image
83 ²⁶. In the original study, Ullman and colleagues tested stimuli at many different levels of degradation and
84 observed that there were critical levels of degradation that led to a sharp drop in performance. They
85 operationally defined MIRCs as image patches that could be reliably recognized on average by human
86 observers and for which further reduction in either size or resolution made the patch unrecognizable. A
87 non-recognizable descendant of a MIRC image was called a sub-MIRC (**Figure 1C**).

88 In our experiments, we presented image patches at different levels of degradation. To minimize
89 potential adaptation effects, stimuli were presented in a mini-block design paradigm. Within each mini-
90 block, images from two out of the ten categories were presented starting from the most degraded stimuli
91 (sub-MIRCs, red in **Figure 1C**), followed by MIRCs (blue in **Figure 1C**), and then the original
92 (undegraded) images (object, black in **Figure 1C**). The same sub-MIRC stimuli were shown again at the
93 end of each mini-block (sub-MIRC post, dashed red in **Figure 1C**). Each participant completed 5
94 consecutive mini-blocks so as to present stimuli from all 10 categories. The order of presentation of the
95 categories was randomized across participants.

96 **Figure 1D** shows recognition performance across our pool of 12 participants. Consistent with the
97 experimental results in Ullman et al.'s study and with the definition above, there was a large drop in
98 performance between MIRC and sub-MIRCs ($p < 0.01$, paired t-test). Notably, this drop was sharp and
99 similar to that measured in the general population (71% drop in the general population²⁶, 87% drop in
100 **Figure 1D**). Furthermore, here we observed a substantial increase in performance between the initial and
101 the final sub-MIRC blocks ("sub-MIRC" and "sub-MIRC post" conditions in **Figure 1D**, 78% increase,
102 $p < 0.01$, paired t-test). That is, the same images that were unrecognizable in the first block (sub-MIRC
103 condition) became recognizable, almost on par with the MIRC images themselves, after exposure to the
104 MIRC and object images (sub-MIRC post condition). This result demonstrates a rapid increase in
105 recognition rates of the sub-MIRC images after presentation of MIRC and object images in the previous
106 blocks. Taken together, the results of **Figure 1D** suggest that our pool of patients, although necessarily
107 smaller than the original large cohort reported in Ullman et al.'s study, showed behavior concordant with
108 that of the general population. In addition, these results demonstrate a rapid and substantial increase in the
109 recognition of sub-MIRC images, after exposure to their associated MIRC and undegraded versions.

110

111 **Minimal image changes between MIRCs and sub-MIRCs elicited large differences in neural** 112 **responses**

113 To investigate the neural representation of MIRC and sub-MIRC stimuli, we implemented several
114 changes in the experimental paradigm compared to the original work by Ullman and colleagues²⁶
115 (**Methods**): (i) while the original study was based on across-participant averages, here we focus on within-
116 participant comparisons; (ii) because of the within-participant design, we first determined the perceptual
117 threshold between MIRC and sub-MIRC stimuli separately for each image and participant; (iii) to assess
118 the reliability of neural responses, each stimulus was repeated 10 times, (iv) to ensure that we could reliably
119 measure neural responses to sub-MIRCs without any learning, the sub-MIRC stimuli were presented before
120 the MIRC stimuli.

121 We first investigated the neural correlates of the perceptual differences between the recognized
122 MIRC and the unrecognized sub-MIRC stimuli. An electrode was considered to be visually selective if it
123 was responsive to either MIRC or sub-MIRC stimuli and the intracranial field potentials (IFPs) elicited by
124 the MIRC images were significantly different from those elicited by the sub-MIRC stimuli for at least 50
125 consecutive ms in the interval [50,550]ms after stimulus onset (see **Methods**).

126 **Figure 2** shows a representative electrode located in the left inferior frontal cortex (**Figure 2A**).
127 Consistent with previous neurophysiological recordings²⁹, this electrode showed strong evoked responses

128 shortly after presentation of the visual stimuli. These responses were stronger for MIRC (blue) and object
129 (black) stimuli, as shown by the large change in IFPs after stimulus onset with respect to the preceding
130 baseline (see average responses in **Figure 2B** and raster plots showing responses in individual trials in
131 **Figure 2C**). Furthermore, the neural responses were significantly different for MIRCs versus sub-MIRCs
132 in the time interval marked by the black horizontal line (**Figure 2D**) and for object vs sub-MIRC in a similar
133 interval (**Figure 2B**). We also observed a trend toward a difference between sub-MIRC post vs. sub-MIRC
134 stimuli that did not pass our strict statistical criteria (**Figure 2E**). It is important to emphasize that, at the
135 pixel level, the difference between the MIRC and sub-MIRC stimuli is minimal (**Figure 1C**). Yet, the two
136 stimuli led to considerable differences both at the behavioral (**Figure 1D**) and neural (**Figure 2D**) levels.
137 Across the entire dataset, we observed electrodes that distinguished MIRCs and sub-MIRC images, like the
138 example in **Figure 2**, over an extended network mostly encompassing the temporal (n=48, 20% of
139 responsive electrodes in that area) and frontal (n=58, 29% of responsive electrodes) cortices (**Figure 3A**).
140 A small number of selective electrodes were also found in the occipital (n=11, 10% of responsive
141 electrodes) and parietal (n=9, 9% of responsive electrodes) cortices.

142 We next evaluated the time at which differential responses between MIRCs and sub-MIRCs
143 emerged. The median time of emergence of selective responses for MIRC versus sub-MIRC stimuli was
144 shorter in the temporal lobe (median=343ms) compared to the frontal lobe (median=368ms), with no
145 statistically significant difference between the two areas (**Figure 3B**, Mann-Whitney U-test=1599, p=0.19,
146 **Methods**). Examination of onset times for responses selective to MIRCs compared to sub-MIRCs in frontal
147 areas revealed that they were not unimodally distributed (Hartigan's dip test = 0.1, p=0.0002³⁰). Indeed,
148 the distribution of the times when selectivity started across different electrodes revealed two components:
149 a first "early" component with onset times smaller than 420ms (n=34 electrodes, median=329ms) and a
150 second "late" component with onset times greater than 420ms (n=24 electrodes, median=478ms; **Figure**
151 **S6**). Interestingly, the median onset time of early responses in frontal regions (median=329ms) was
152 significantly shorter than the median onset time in temporal regions (Mann-Whitney U-test=580, p=0.021),
153 which, in turn, was shorter than the median onset time of late frontal responses (Mann-Whitney U-
154 test=1029, p=6.4·10⁻⁸). Due to limited electrode sampling, this bimodality could only be verified in a single
155 participant when examining the onset of selective responses at the individual participant level.

156 These results suggest that during recognition of MIRC stimuli the emergence of selective responses
157 in frontal areas can precede that in temporal areas. To further investigate this point, we used functional
158 interaction analysis to evaluate the temporal dynamics of the activation of temporal and frontal areas during
159 recognition of MIRC stimuli. To have sufficient statistical power, we focused on the participants that had
160 more than one responsive electrode in both the temporal and frontal lobes (n=6 participants) and we used

161 generalized Partial Directed Coherence (gPDC, ^{31,32}) to assess the information flow between the frontal and
162 temporal lobes. gDPC provides a measurement of the directed linear relationship between pairs of time
163 series, allowing to quantitatively compare the strength, directionality, and statistical significance of
164 interactions between areas (see **Methods**). The two curves in **Figure 4A** show the average of the gDPC
165 across subjects and pairs of frontal and temporal electrodes (n=3,639 electrode pairs), and thus of the
166 information flow, in the frontal to temporal (green curve) and temporal to frontal (blue curve) directions,
167 respectively, with red shaded areas signifying time intervals when the two curves are significantly different
168 ($p < 0.05$ based on a bootstrapping analysis, see **Methods**). In the time interval immediately following the
169 presentation of MIRC stimuli, gPDC was significantly stronger in the top-down fronto-temporal direction
170 (red shaded areas in **Figure 4A**). This prevalence of a top-down fronto-temporal directionality disappeared
171 shortly after 300ms after MIRC presentation, and, after that time, the flow of information was either
172 significantly stronger in the opposite bottom-up temporo-frontal direction or equally strong in the two
173 directions (**Figure 4A**). Next, we computed, for each frontal electrode, the time at which the functional
174 interactions to and from all paired temporal electrodes was significantly stronger in either the frontal-
175 temporal or temporal-frontal direction. As shown by the two distributions in **Figure 4B**, the median onset
176 time at which the interactions were significantly stronger in the frontal to temporal direction was
177 significantly earlier than when it was stronger in the temporal to frontal direction (median
178 frontal \rightarrow temporal=96ms, median temporal \rightarrow frontal=312ms; Mann-Whitney U-test=675, $p=0.028$).

179

180 **Neural changes accompanied learning to recognize sub-MIRC images**

181 Participants could not recognize sub-MIRC stimuli when presented in the first part of each mini-
182 block. However, these same stimuli became recognizable after exposure to the MIRC and object images
183 (**Figure 1D**). We next asked how this rapid increase in recognition performance was reflected in the neural
184 signals by comparing the IFP responses to sub-MIRC post versus sub-MIRC stimuli.

185 The example electrode in **Figure 2** showed a significant difference between the responses to
186 MIRC versus sub-MIRCs (**Figure 2D**) and a trend toward a difference between the sub-MIRCs post versus
187 sub-MIRCs which did not reach statistical significance (**Figure 2E**). The example electrode in **Figure 5**,
188 located in the in the inferior temporal cortex (Figure 5A), exhibited strong evoked responses during the
189 presentation of MIRC (blue) and also during presentation of sub-MIRC post (dashed red) stimuli (**Figure**
190 **5B**). Similar to the electrode in Figure 2, the electrode in Figure 5 distinguished MIRC from sub-MIRC
191 stimuli (**Figure 5D**). In contrast to the example electrode in Figure 2, the electrode in Figure 5 also exhibited
192 a significantly different response to sub-MIRC post vs. sub-MIRC images (**Figure 5E**). These differences
193 were also evident in single trials (**Figure 5C**). Notably, sub-MIRC post and sub-MIRC stimuli are identical.

194 Thus, this difference in neural responsiveness reflects the rapid and unsupervised learning processes that
195 made sub-MIRC post stimuli recognizable.

196 A comparison of the neural responses to sub-MIRC post versus sub-MIRC stimuli across all
197 electrodes revealed selective responses reflecting recognition primarily for electrodes located in the
198 temporal lobe (n=17, 9% of responsive electrodes in that area). A small number of selective electrodes was
199 also found in occipital (n=6, 6% of responsive electrodes in that area), parietal (n=6, 10% of responsive
200 electrodes in that area) and frontal (n=5, 5% of responsive electrodes in that area) lobes (**Figure 6A**). The
201 median onset times of selective responses to sub-MIRC post versus sub-MIRC stimuli in the temporal lobe
202 was 252ms (**Figure 6B**).

203

204 **Discussion**

205 We recorded neurophysiological responses from the human brain during recognition of Minimally
206 Recognizable Configuration (MIRC) images and sub-MIRCs²⁶. MIRCs and sub-MIRCs exhibit small
207 differences at the pixel level. Yet, the participants showed a dramatic perceptual transition, recognizing
208 MIRCs while failing to recognize sub-MIRCs (**Figure 1D**). After exposure to the MIRC and object stimuli,
209 participants could recognize the same sub-MIRC images that they could not recognize initially (**Figure**
210 **1D**). These behavioral observations were accompanied by temporally- and spatially-specific neural
211 responses. Selective responses to MIRCs emerged in frontal and temporal cortex and the interactions
212 between these two areas switched from an earlier frontal to temporal direction to a later temporal to frontal
213 direction (**Figures 3, 4**). Furthermore, the rapid increase in recognition of sub-MIRCs was associated with
214 the emergence of selective responses predominantly in the temporal lobe (**Figures 5, 6**).

215 In our experiments, the frontal lobe appeared to have an important role in the recognition of MIRC
216 stimuli. A role of this brain region in the perception, recognition and categorization of objects³³ is supported
217 by experiments in monkey showing that frontal cortex contains neurons selective for complex visual stimuli
218³³⁻⁴⁰. In particular, frontal areas seem to be specifically involved in the processing of challenging stimuli,
219 such as ambiguous, occluded or masked objects^{23,24,41-43}. For instance, monkey prefrontal cortex neurons
220 are more activated by occluded objects that are hard to identify⁴⁴ and inactivation of ventral pre-frontal
221 cortex impairs encoding and recognition of challenging images^{45,46}. Furthermore, frontal areas seem to
222 have a role in the learning and retrieval of perceptual categories⁴⁷⁻⁵². MIRC images are, by definition,
223 challenging to recognize as they contain only minimal information about the depicted object and their
224 recognition entails long integration times⁵³. In line with that, **Figures 3** and **4** suggest that recognition of
225 MIRC stimuli is associated with an initial top-down functional interaction from the frontal to the temporal

226 lobe followed by a later bottom-up interaction in the opposite direction. This result is corroborated by a
227 frequency-resolved gDPC analysis showing that, in agreement with recent proposals^{54–57}, the initial frontal
228 to temporal flow of information is carried by lower temporal frequencies in the beta range, while the later
229 temporal to frontal flow of information is mainly carried out by higher temporal frequencies in the gamma
230 range (**Figure S8**). Interestingly, a functional interaction analysis on the sub-MIRC trials revealed only a
231 feedforward flow of information from temporal to frontal areas (**Figure S3**). This result might seem at odds
232 with the intuition that the unrecognized sub-MIRC stimuli could produce “hypotheses” in the frontal cortex
233 that are fed back to temporal areas without reaching confirmation. However, the functional interactions
234 analysis reveals directed interactions between neural responses in frontal and temporal areas. In the case of
235 sub-MIRCs, there is a feedforward interaction between temporal and frontal responses that is related to
236 visual processing of these stimuli. The opposite frontal to temporal interactions are missing, perhaps
237 because any activity in frontal areas related to “hypotheses formulation” did not produce a corresponding
238 recognition-related activity in temporal areas given that sub-MIRC stimuli were, by definition, not
239 recognized.

240 The frontal lobe is also implicated in speech production⁵⁸. It might be thus hypothesized that the
241 selective responses that we observed in frontal areas might be, at least partially, due to the preparatory
242 activity related to the task of verbally reporting their percept that the participants had to carry out. Two
243 reasons make this interpretation of our results unlikely. First, our participants had to verbally report their
244 percept in all conditions. The results of **Figure 3** were obtained by contrasting IFPs produced by MIRC
245 stimuli with those produced by sub-MIRC stimuli and this contrast should thus discount potential neuronal
246 activations related to speech preparation that are common to the two conditions. Second, the contrast sub-
247 MIRC post vs sub-MIRC (**Figure 6**) produced virtually no selective responses in frontal areas. Participants
248 had to verbally report their percept also in these two conditions and the recognition rates of sub-MIRC post
249 stimuli were also comparable to those of MIRC stimuli (**Figure 1D**), that produced instead widespread
250 selective responses in the frontal lobe (**Figure 3**).

251 Perception of MIRC stimuli elicited widespread activations also in the temporal lobe (**Figure 3**).
252 This brain region has also been implicated in the recognition of occluded and ambiguous stimuli. Indeed,
253 studies have shown signals in the human inferior temporal cortex that may reflect the processing of occluded
254 stimuli^{20,23,24,59–61}. In the same vein, studies in monkeys have identified populations of neurons in infero-
255 temporal cortex whose responses correlated with the spatial extent of the occluder or that declined with the
256 degree of occlusion of a to-be-recognized shape^{44,62–64}. The selective responses for MIRCs that we found
257 in the temporal lobe might thus also reflect the activation of neural processes involved in their recognition.
258 This proposal is also consistent with a neuroimaging study in humans that showed, in agreement with results

259 reported here, that the MIRC vs sub-MIRCs contrast generated extensive activations in several regions of
260 the temporal lobe ⁶⁵. Taken together, the pattern of activations during the perception of MIRC stimuli
261 suggests that their recognition might rely on the dynamic interplay of fronto-temporal neural processes.

262 Participants quickly learned to recognize sub-MIRC images after being exposed, in previous blocks
263 and with no feedback, to the associated MIRC and object images (**Figure 1D**). This striking difference in
264 recognition performance was correlated with concomitant changes in the neural responses, predominantly
265 in the temporal lobe (**Figures 5,6**). Because the sub-MIRC post stimuli are, by definition, identical to the
266 sub-MIRC stimuli presented initially, these neural responses reflect the participant's distinct perceptual
267 experience between the initial and subsequent encounters with these complex stimuli. The results are
268 reminiscent of a very interesting study by Tovee et al. ⁶⁶ in which they found a change in the responses of
269 single units in the macaque temporal lobe during the observation of degraded visual stimuli before and after
270 exposure to their undegraded and fully recognizable versions.

271 Consistent with the fact that MIRC and sub-MIRC images are very similar at the pixel level ²⁶, their
272 contrast produced a low number of selective responses in low-level areas in the occipital lobe (n=11, **Figure**
273 **3**). In agreement with this observation, an even lower number of selective responses in occipital cortex was
274 produced by the contrast sub-MIRC post vs sub-MIRC (n=6, **Figure 6**), where the presented stimuli were
275 indeed the same in both conditions. These results are in agreement with the notion that the occipital lobe is
276 mainly involved in the processing of low-level characteristics of visual stimuli ⁶⁷ and further strengthen the
277 conclusion that recognition of MIRC stimuli relies on high-level, rather than low-level, mechanisms.

278 For both MIRC and sub-MIRC post stimuli, the median time at which selective neural signals
279 emerged in the temporal lobe was around 250-350ms (**Figures 3 and 6**), which is longer than the typical
280 latencies of 100-200ms reported for the decoding of object identity from population responses ^{29,68,69}. At
281 the behavioral level, MIRC stimuli are known to produce long response times which might be the result of
282 long integration processes ^{53,70}. Here, we specifically focused on these recognition processes by comparing
283 IFPs elicited by recognized stimuli (MIRC or sub-MIRC post) versus those elicited by the unrecognized
284 sub-MIRC stimuli in the interval from 50 to 550ms after stimulus onset. In contrast, many earlier studies
285 focused on the neural responses to easy-to-recognize stimuli ⁶⁹ in a shorter temporal window (e.g. [50,
286 300]ms ^{29,68} after stimulus onset. Thus, the longer median onset time that we found may be related to the
287 accumulation of evidence that is needed to recognize the challenging MIRC stimuli and the relatively long
288 search interval that we considered. In line with this interpretation, long latencies, similar to those reported
289 here, have been reported in previous human studies that investigated perceptual closure processes by
290 contrasting, similar to our approach, challenging-to-recognize stimuli versus unrecognized stimuli ^{20,59,60,71}

291 or the timing of conscious perception^{72–75} in a large temporal window after stimulus onset. Indeed, as shown
292 in **Figure S4**, visual responses to MIRC stimuli (i.e. MIRC responses significantly different from baseline)
293 in the [50, 350]ms interval exhibited a sensibly shorter median latencies (median =152ms and 208ms in the
294 occipital and temporal lobe respectively, **Figure S4A**) that are in line with previous decoding studies, with
295 several of these responses starting already before 100ms (**Figure S4B**).

296 **Limitations of the study**

297 In Ullman *et al.*'s original study on minimally recognizable configurations, each participant was
298 exposed to a single stimulus for each category and was never tested again; thus, all the comparisons were
299 between participants²⁶. Our study focused on the neural responses to such stimuli and therefore several
300 changes were introduced with respect to the original experimental design. Our study focuses on
301 comparisons within participants, which required presenting different levels of degradation of the original
302 images in sequential order: as shown in **Figure 1D**, participants recognize sub-MIRC images after exposure
303 to the MIRC and object images. To ensure reproducibility, stimuli are repeated multiple times in contrast
304 to the single presentations in Ullman *et al.*'s original work (**Methods**).

305 All the neural data in our study come from patients with pharmacologically-resistant epilepsy. As
306 a consequence, the number and location of electrodes are dictated solely by clinical criteria. Although we
307 had extensive coverage of brain locations (**Table S1, Figure S1 and S7**), this sampling was necessarily not
308 exhaustive. Thus, other regions, not sampled here, may also contribute to processing MIRC, sub-MIRC,
309 and sub-MIRC post stimuli.

310 The age range in our study is limited by the availability of patients with pharmacologically-resistant
311 epilepsy. Previous developmental studies show that, by the age of 11, visual object perception has several
312 adult-like behavioral characteristics^{76,77}. Additionally, the behavioral results in Figure 1D are consistent
313 with previous work²⁶. However, it is possible that a much larger sample of patients at different ages could
314 help better delimit the development of interactions between ventral visual cortex and frontal cortex regions
315 during recognition of complex images.

316

317 **Conclusions**

318 There has been exciting progress in developing computational models that provide a first-order
319 approximation to the cascade of computations along the ventral visual cortex during object recognition<sup>78–
320 81</sup>. These models can capture aspects of visual recognition behavior in monkeys and humans⁸² and can also
321 approximate neural responses along the ventral visual cortex⁸³. Despite these successes, multiple pieces of
322 evidence have highlighted that these models fail to account for the whole repertoire of visual behavior and
323 neurophysiology^{84,85}. In particular, these models fail to account for recognition of MIRC stimuli²⁶.

324 Challenging stimuli like MIRC_s, and especially the sharp transition from sub-MIRC to MIRC in the neural
325 and behavioral responses, provide important constraints to develop future models that incorporate recurrent
326 computations hypothesized to be critical for recognition.

327

328 **Resource availability**

329 **Lead contact.** Gabriel Kreiman (Gabriel.kreiman@tch.harvard.edu)

330 **Materials availability.** This study did not use or generate any reagents.

331 **Data and code availability.** All the data and code are publicly available through the following website:

332 <https://kreimanlab.com/code/mirc/>

333

334 **Acknowledgments.** We thank all the patients for participating in these experiments. This work was
335 supported by BSH-NSF Grant 1746365 (SU and GK), NIH grant R01EY026025 (GK), by the Center for
336 Brains, Minds and Machines (SU and GK).

337

338 **Author contributions.** The experiments were designed by SU, GBY, JGK, and GK. SS and JRM
339 performed the surgeries. JGK collected the data. Data analyses were performed by AC, AuC and JGK. The
340 manuscript was written by AC, AuC and GK, with feedback and approval from all the authors.

341

342 **Declaration of interest.** The authors have no conflicts of interest to disclose.

343

344

345

346

347 **Figure legends**

348 **Figure 1 – Experimental design and behavioral performance.** (A) Temporal unfolding of each trial. A trial
349 started either 3 seconds after the end of the previous trial or upon a key press from the participant. A
350 fixation cross was first shown for 400 ms, followed by an image shown for 1 second. After the image
351 disappeared, the participant was asked to verbally identify the image. (B) The 10 images of objects or
352 objects parts used as base stimuli. (C) Temporal order of the conditions presented in the experiments. MIRC
353 (Minimal Recognizable Configurations, blue) and sub-MIRC (red) stimuli were images obtained by cropping
354 or changing the resolution of the base images. MIRC images were defined as image patches that are
355 reliably recognized by observers and for which further reduction in either size or resolution makes the patch
356 unrecognizable. A non-recognizable descendant of a MIRC image was called a sub-MIRC²⁶. Object (black)
357 stimuli were a subset of the base images in B. The sub-MIRCs post (dashed red) stimuli consisted of the
358 same sub-MIRCs images from block 1, presented again at the end of the experiment, after participants
359 were exposed to the MIRC and object images. (D) Recognition performance (fraction correct) for each
360 stimulus condition (n=12 participants). Notice the sharp drop in performance between MIRC (blue) and
361 sub-MIRC (red) images and the increased performance in the sub-MIRC post (red stripes) compared to the
362 sub-MIRC images. Error bars represent standard error of the mean.

363 **Figure 2 – Neural responses distinguished MIRCs from sub-MIRC images.** (A) Example electrode in the
364 triangular part of the left inferior frontal gyrus shown on a template brain (MNI coordinates = [-53.4, 27.9,
365 11]). (B) Neural responses of the example electrode in the four experimental conditions (Fig. 1C): object
366 (black), MIRC (blue), sub-MIRC (red) and sub-MIRC post (dashed red). The curves represent the mean
367 intracranial field potential (IFP) response in each condition, aligned to stimulus onset (t=0, vertical black
368 dashed line) and averaged across all trials. The shaded area around each curve indicates standard error of
369 the mean. The number of trials in the different conditions are shown in the legend at the bottom. The gray
370 rectangle marks the interval considered for the analysis of neural responses. (C) Same responses as in panel
371 B, showing all individual trials as raster plots (see scale bar in color map on the right). The color of each
372 box's border indicates the experimental condition. (D, E) Responses to MIRC and sub-MIRC stimuli (D), and
373 sub-MIRC post and sub-MIRC stimuli (E). The black horizontal line in D shows the interval in which
374 responses to MIRCs and sub-MIRCs were statistically different (p<0.01, Mann-Whitney U-test).

375 **Figure 3 - Selective responses to MIRCs vs sub-MIRCs exhibited spatial and temporal specificity.** (A)
376 Locations of electrodes exhibiting significantly different responses between MIRCs and sub-MIRCs (n=156).
377 Selective responses were mostly located in the temporal (n=48) and frontal (n=58) cortex. Each circle
378 represents an electrode; the color codes the time at which an electrode started to differentiate between
379 MIRCs and sub-MIRCs. (B) Distribution of selectivity start times for the MIRC vs. sub-MIRC comparison in
380 the frontal and temporal lobes (median temporal lobe=343ms; median frontal lobe=368ms). The
381 distributions of onset times for electrodes located in the occipital and parietal cortex were not plotted here
382 since only n=11 and n=9 electrodes, respectively, were found. The brain locations of the remaining n=30
383 electrodes could not be determined.

384

385 **Figure 4 – Temporal dynamics of the functional interactions between temporal and frontal areas during**
386 **the perception of MIRC stimuli.** (A) Strength, as assessed by generalized Partial Directed Coherence (gDPC
387 ³¹), of the temporal to frontal (blue curve) and frontal to temporal (green curve) functional interactions
388 measured in participants (n=6) that had at least 2 responsive electrodes in both the temporal and frontal

389 lobe. The curves represent the average gPDC obtained from n=3639 pairs of frontal and temporal
390 electrodes respectively. Standard errors are shown but they are too small to be visible. Red-shaded areas
391 mark intervals where the interactions in one direction are significantly stronger than in the opposite
392 direction. The functional interactions are initially stronger in the frontal to temporal direction and they
393 subsequently (after approximately 400ms) become either equally strong in the two directions or stronger
394 in the temporal to frontal direction. **(B)** Distributions, across all examined frontal electrodes, of the onset
395 times at which the functional interactions were stronger in the frontal to temporal compared to the
396 opposite temporal to frontal direction (green) or the other way around (blue). The medians of the two
397 distributions were significantly different (Mann-Whitney U-test=675, p=0.028. Frontal → temporal:
398 median = 96ms; Temporal → frontal: median = 312ms).

399 **Figure 5 – Selective responses to sub-MIRC post versus sub-MIRC images.** Example electrode in the left
400 inferior temporal cortex (MNI coordinates = [-32.7, -27.1, -23.6]). The layout of the panels and symbols
401 follow the format in **Figure 2**. This electrode showed a significantly different response between sub-MIRC
402 post (dashed red) and sub-MIRC (red) **(E)** and between MIRC (blue) and sub-MIRC (red) **(D)**.

403

404 **Figure 6 – Sub-MIRCs post stimuli elicited selective responses in the temporal lobe.** Locations of
405 electrodes exhibiting significantly different responses between sub-MIRC post and sub-MIRC images
406 (n=39). Selective responses were mostly located in the temporal cortex (n=17). **(B)** Distribution of start
407 times for selective responses for the sub-MIRC post vs. sub-MIRC comparison in the temporal cortex
408 (median=252ms). The distributions of onset times for electrodes located in the frontal, parietal and
409 occipital cortex are not shown since only n=5, n=6 and n=6 electrodes, respectively, were found.

410

411 STAR Methods

412 Key resources table

Software and algorithms		
Python 3.12.7	Python Software Foundation	https://www.python.org/
Matlab R2024	The MathWorks, Inc., Natick, MA	https://www.mathworks.com
FreeSurfer 6	⁸⁶	https://surfer.nmr.mgh.harvard.edu/
Intracranial Electrode Visualization (iELVis) Toolbox	⁸⁷	https://github.com/iELVis/iELVis
generalized Directed Partial Coherence (gDPC)	^{31,32}	
Custom code developed in this study	DOI: 10.5281/zenodo.14788055	https://kreimanlab.com/code/mirc/

413

414 Resource availability

415 Raw data and the code developed for data analysis are available at <https://kreimanlab.com/code/mirc/>
 416 and also DOI: 10.5281/zenodo.14788055

417

418 Materials availability

419 This study did not use or generate any reagents.

420

421

422 Experimental model and study participant details

423 Participants were 12 patients (5 male, 11–43 years old, see **Table S2**) with pharmacologically-
424 resistant epilepsy treated at Children's Hospital Boston (CHB) or John Hopkins Hospital (JHH). The patients
425 were implanted with intracranial electrodes to localize seizure foci for potential surgical resection^{29,88}. All
426 procedures were approved by each hospital's institutional review board and were carried out with the
427 participants' informed consent. Electrode types, numbers, and locations were driven solely by clinical
428 considerations.

429

430 Methods

431 Psychophysics task

432 Participants had to identify grayscale images presented at the center of a Mac Pro 15-inch laptop's
433 screen placed in front of them. Stimuli were presented with a uniform gray ([128, 128, 128]) background,
434 at an estimated screen luminance of around 150 nits. The sequence of events within each trial is shown in
435 **Figure 1A**. Participants were first presented with a black fixation cross on a gray screen. After 400ms, the
436 fixation cross disappeared, and an image was presented at the center of the screen for 1s. Images were
437 200 × 200 pixels in size and subtended approximately 5x5 degrees of visual angle. Finally, patients were
438 shown a blank screen with a question mark and asked to report verbally with a single word what they
439 recognized in the image. The experimenter compared these single-word responses with a list of acceptable
440 words for each image to assess correctness. The list of acceptable words was created by asking a different
441 set of participants in the lab to describe the full object images with single words using unlimited
442 presentation time. The participants' responses were recorded, and no feedback about their correctness
443 was provided. In total, 5,444 images were presented across all participants.

444

445 Visual stimuli

446 The images presented in our experiment were a subset of those used in the original Ullman *et al.*
447 study²⁶. The images were generated starting from a set of 10 images representing objects or object parts
448 from ten different categories (**Figure 1B**: plane, ship, fly, eagle, horse, bike, car, eye, eyeglasses, and suit).
449 For each image, Ullman *et al.* generated five descendants belonging to two types obtained by iteratively
450 cropping it or resampling it at a lower resolution respectively. They operationally labeled an image a "MIRC"

451 if “it could be reliably identified by a human observer and none of its five descendants could reach a
452 recognition criterion of 50%”²⁶. A non-recognizable descendant of a MIRC is referred to as “sub-MIRC”.
453 Images could thus only post-hoc be labeled as MIRC or sub-MIRC. The combination of the similarity at the
454 pixel with the dramatic difference in recognition rates of MIRC and sub-MIRC stimuli make them ideal
455 candidates to probe the differences in neural processes between recognized and unrecognized stimuli.

456 Ullman *et al.*'s original behavioral experiment was run online on Amazon's Mechanical Turk and
457 sampled a large population of approximately 14,000 participants²⁶. Comparisons were made across
458 participants who were exposed to each image only once. Our focus was to evaluate the neural responses
459 to those images and we therefore introduced several modifications to the task. In Ullman *et al.*'s
460 experiments, each participant viewed only one image. In our experiments, each participant was presented
461 with images from all the 10 categories (“object” condition in **Figure 1D**) together with three of its
462 descendants at progressively higher levels of degradation. To minimize adaptation effects, stimuli were
463 presented in a mini-block design paradigm. Within each mini-block, we presented stimuli belonging to two
464 out of the ten stimulus categories starting from the most degraded to the undegraded images (“object”
465 condition) (**Figures 1C**). The most degraded stimuli were presented again at the end of the mini-block (“sub-
466 MIRC post” condition). Each participant underwent 5 consecutive mini-blocks so as to present all 10
467 stimulus categories. The order of presentation of the 10 categories was randomized across participants.
468 For subject 1, stimuli were presented in a standard block design with no mini-blocks. In a separate
469 psychophysics experiment with 7 participants without epilepsy, we verified that this modified experimental
470 design did not alter recognition performance and yielded results similar to the original study (**Figure S2**).

471 Following Ullman *et al.*²⁶, for each category and participant, we labeled “MIRCs” all images whose
472 recognition performance was higher than 50% and “sub-MIRCs” all images that yielded a recognition rate
473 smaller than 50%. This step defined, on a participant-by-participant level, the threshold for which a
474 recognizable visual stimulus (i.e., a MIRC) becomes unrecognizable (i.e., a sub-MIRC). For each participant,
475 image categories for which this was not possible (i.e., that produced a recognition rate consistently higher
476 or lower than 50% at all levels of degradation) were excluded from further analyses. In the “MIRC” and
477 “sub-MIRC” blocks, each participant was shown each image for 10 times for a total of 200 trials (10
478 categories x 2 conditions (MIRC and sub-MIRC) x 10 repetitions). In the “object” and “sub-MIRC post”
479 blocks, each participant was shown each image for 5 times for a total of 100 trials (10 categories x 2
480 conditions (object and sub-MIRC post) x 10 repetitions). The original Ullman *et al.* study only defined MIRC
481 and sub-MIRC *on average, across participants*. However, for the evaluation of neural responses, it is

482 essential to define whether a given participant recognized an image or not. For example, a given sub-MIRC
483 image could yield, say, 15% recognition and the corresponding MIRC image could yield, say, 90%
484 recognition, on average across participants, which would be consistent with the strong behavioral effects
485 reported in Figure 1D and in the original study. However, here we are particularly interested in whether a
486 given individual participant did or did not recognize a given image and it would thus not suffice to use the
487 average behavioral assessments.

488

489 Neurophysiological recordings

490 Participants were implanted with either intracortical stereo electroencephalography (sEEG) depth
491 electrodes or subdural electrocorticography (ECoG) electrodes (Ad-Tech, Racine, WI, USA). Depth
492 electrodes contained from 6 to 16 recording sites. Each subdural grid or strip had from 4 to 128 recording
493 sites with an inter-site distance of 1 cm. Each recording site was 2 mm in diameter. The number of recording
494 sites per participant ranged from 83 to 229, for a total of 1,752 sites across all participants (see **Table S1** for
495 the electrodes for which brain location could be recovered). All data were collected during periods without
496 seizures. Data were recorded using XLTEK (Oakville, ON, Canada) or BioLogic (Knoxville, TN, USA) with
497 sampling rates of 1,000 Hz or 2,000 Hz, depending on the hospital. For analysis purposes, all signals were
498 down-sampled to 1,000 Hz.

499

500 Quantification and statistical analysis

501

502 Data Pre-processing

503 Data analyses were performed in Python. We followed the same pre-processing steps for the
504 intracranial field potentials (IFPs) as in previous studies²⁹. We first applied a notch filter at 60 Hz and
505 harmonics, and we then low-pass filtered the signal at 100 Hz. We excluded from further analysis electrodes
506 that showed evidence of electrical noise. Finally, to remove potential movement artifacts, we computed,
507 on a per-electrode basis, the overall distribution of the total IFP power in all trials for each electrode
508 (regardless of experimental condition) and excluded from further analyses those trials whose power was
509 more than 4 standard deviations from the mean.

510

511 **Electrode localization**

512 Electrodes were localized by co-registering the preoperative magnetic resonance imaging (MRI)
513 with the postoperative computer tomography (CT) by means of the iELVis toolbox for Matlab ⁸⁷. For each
514 participant, the brain surface was reconstructed from the MRI, corrected for post-implant brain shift, and
515 assigned to one of 75 different regions in Freesurfer software ⁸⁶ based on the 2009 atlas ^{29,89,90}. Depth
516 electrodes were assigned either to a subcortical structure or to gyri/sulci. The location of electrodes for
517 which the brain location could be recovered together with their average MNI coordinates is shown in **Table**
518 **S1**.

519 **Data Analysis**

520 **Comparison between conditions** – We first sorted the instantaneous values of the IFPs at time t , $IFP_j(t)$,
521 based on trial j and condition c (i.e., MIRC, sub-MIRC, object or sub-MIRC post). For each condition and
522 participant, we normalized all trials by subtracting the average across trials of the IFPs during the baseline
523 interval ([-200 50] ms before stimulus onset). For each contrast between two conditions $c1$ and $c2$ (e.g.,
524 MIRC vs sub-MIRC), we first identified the set of responsive electrodes, defined as those electrodes whose
525 $IFP_j(t)$ were statistically different from baseline at a $p < 0.01$ level (Wilcoxon ranksum test) for at least 50
526 consecutive time points for either condition $c1$ or condition $c2$. The length of this interval was selected so
527 as to keep the experiment-wide false discovery rate below the $p < 0.05$ threshold throughout all our analyses
528 (see section “Bootstrapping analysis of the number of selective electrodes” and **Figure S5**). We defined
529 visually selective electrodes within the responsive electrodes as those whose distributions $IFP_{j,c1}(t)$ and
530 $IFP_{j,c2}(t)$ during conditions $c1$ and $c2$ respectively, were statistically different at a $p < 0.01$ level for at least 50
531 consecutive time points. The latency of stimulus selectivity was defined as the first time point when the
532 statistical test was significant. We focused on two comparisons: MIRC vs. sub-MIRC and sub-MIRC post vs.
533 sub-MIRC in the time interval [50 550] ms after stimulus onset.

534

535 **Bootstrapping analysis of the number of selective electrodes** – To estimate the null-hypothesis distribution
536 of the number of significant electrodes yielded by a contrast between two conditions $c1$ and $c2$ we first
537 randomly shuffled, within each participant, the labels of the trials belonging to the conditions and we then
538 performed the analysis as detailed above (“Comparison between conditions”). We repeated these steps

539 for 500 times to estimate the null-hypothesis distribution. Comparison of the number of selective
540 electrodes obtained in the two contrasts described here (MIRC vs sub-MIRC: 156 electrodes, and sub-MIRC
541 post vs sub-MIRC: 39 electrodes) with these null-distributions shows that in both cases the false discovery
542 rate (FDR) was < 0.05 (Figure S5).

543

544 **Directional correlation** – To assess the directional correlation between channels, we employed the time-
545 varying generalized Partial Directed Coherence (gPDC)³¹, which is an approach based on the Geweke-
546 Granger causality framework^{91,92}. Among many directional correlation estimation methods such as the
547 Directed Transfer Function, the Partial Directed Coherence, and the multivariate Granger Causality^{32,93,94},
548 the gPDC has been proven to be the most effective estimator and to be robust with respect to the data
549 normalization method^{32,95,96}. Within the Granger causality framework, a time series \mathbf{x} is directionally
550 correlated to a time series \mathbf{y} if the knowledge of past samples of \mathbf{x} reduces the prediction error for the
551 current sample of \mathbf{y} . The relation can be estimated by fitting, for each participant, a time-varying
552 multivariate autoregressive (MVAR) model on the set of available electrodes. In our analyses, the order of
553 the MVAR model was set to 40 (i.e., spanning a 40ms interval) to account for neurophysiologically plausible
554 timing of interactions between areas. Among time-varying MVAR estimation methods, the GLKF
555 outperformed other algorithms, such as the recursive least square, the multivariate adaptive
556 autoregressive estimator, the classic Kalman filter, and the dual extended Kalman filter^{97–100}. It should be
557 noted that we fitted the GLKF on the raw IFPs (i.e. not low-pass filtered), as spurious correlations can arise
558 when time series are filtered¹⁰¹. For each participant, we then used the MVAR model parameters to
559 compute the gPDC between each possible pair of electrodes in the temporal and frontal lobe. We
560 discounted pre-stimulus connectivity by removing from each trial and frequency the average connectivity
561 estimated in the baseline interval. For each electrode pair, the gPDC is a function of time and frequency.
562 We averaged the gPDCs values in the frequency domain to deal only with broadband temporal signals. We
563 then used a cluster-based permutation test¹⁰² to quantitatively compare the strength of the directional
564 correlation from the temporal to the frontal lobe and vice versa across participants and channels. This
565 analysis identified clusters of contiguous time points exhibiting consistent patterns, and permutation
566 testing was applied to determine whether these clusters represented statistically significant deviations
567 from chance.

568

569 **Analysis of the latency of directional correlation** – For each frontal electrode f_i , we conducted a cluster-
570 based permutation test ¹⁰² to compare the mean directional correlation from all temporal electrodes to f_i
571 against the mean directional correlation from f_i to all temporal electrodes. The first time point at which this
572 difference was statistically significant, if present, represented the onset latency of a difference between
573 the directed correlation to or from f_i . Latencies were then sorted into two sets, based on whether they
574 corresponded to a higher gPDC from the temporal lobe to f_i or from f_i to the temporal lobe (the two
575 distributions in **Figure 4B**). A subsequent Mann-Whitney U test was employed to assess the significance of
576 the difference in latency distributions of the medians between these two sets.

577

578

579 **References**

- 580 1. Riesenhuber, M., and Poggio, T. (2000). Models of object recognition. *Nat. Neurosci.* 3, 1199–
581 1203.
- 582 2. Peissig, J.J., and Tarr, M.J. (2007). Visual object recognition: Do we know more now than we did
583 20 years ago? *Annu. Rev. Psychol.* 58, 75–96.
584 <https://doi.org/10.1146/annurev.psych.58.102904.190114>.
- 585 3. Biederman, I., and Gerhardstein, P.C. (1993). Recognizing depth-rotated objects: Evidence and
586 conditions for three-dimensional viewpoint invariance. *J. Exp. Psychol. Hum. Percept. Perform.*
587 19, 1162–1182. <https://doi.org/10.1037/0096-1523.19.6.1162>.
- 588 4. Biederman, I., and Cooper, E.E. (1991). Evidence for Complete Translational and Reflectional
589 Invariance in Visual Object Priming. *Perception* 20, 585–593. <https://doi.org/10.1068/p200585>.
- 590 5. Alais, D., Blake, R., and Lee, S.-G. (1998). Visual features that vary together over time group
591 together over space. *Nat. Neurosci.* 1, 160–164. <https://doi.org/10.1038/414>.
- 592 6. Gerbino, W., and Salmaso, D. (1987). The effect of amodal completion on sequential matching.
593 *Acta Psychol. (Amst).* 65, 25–46.
- 594 7. Rensink, R.A., and Enns, J.T. (1998). Early completion of occluded objects. *Vision Res.* 38, 2489–
595 2505. [https://doi.org/10.1016/S0042-6989\(98\)00051-0](https://doi.org/10.1016/S0042-6989(98)00051-0).
- 596 8. Blake, R., and Lee, S.-H. (2005). The role of temporal structure in human vision. *Behav. Cogn.*
597 *Neurosci. Rev.* 4, 21–42. <https://doi.org/10.1177/1534582305276839>.
- 598 9. Snodgrass, J.G., and Feenan, K. (1990). Priming effects in picture fragment completion: Support
599 for the perceptual closure hypothesis. *J. Exp. Psychol. Gen.* 119, 276–296.
600 <https://doi.org/10.1037/0096-3445.119.3.276>.
- 601 10. Foley, M.A., Foley, H.J., Durso, F.T., and Smith, N.K. (1997). Investigations of closure processes:
602 What source-monitoring judgments suggest about what is “closing.” *Mem. Cognit.* 25, 140–155.
603 <https://doi.org/10.3758/BF03201108>.
- 604 11. Gollin, E.S. (1962). Factors Affecting the Visual Recognition of Incomplete Objects: A
605 Comparative Investigation of Children and Adults. *Percept. Mot. Skills* 15, 583–590.
606 <https://doi.org/10.2466/pms.1962.15.3.583>.
- 607 12. Gauthier, I., and Tarr, M.J. (2016). Visual object recognition: Do we (finally) know more now
608 than we did? *Annu. Rev. Vis. Sci.* 2, 377–396. <https://doi.org/10.1146/annurev-vision-111815-114621>.
- 610 13. Ungerleider, L.G., and Bell, A.H. (2011). Uncovering the visual “alphabet”: Advances in our
611 understanding of object perception. *Vision Res.* 51, 782–799.
612 <https://doi.org/10.1016/j.visres.2010.10.002>.
- 613 14. Casile, A., and Giese, M.A. (2005). Critical features for the recognition of biological motion. *J.*
614 *Vis.*, 348–360. <https://doi.org/10.1167/5.4.6>.
- 615 15. Ullman, S., Vidal-Naquet, M., and Sali, E. (2002). Visual features of intermediate complexity and
616 their use in classification. *Nat. Neurosci.* 5, 682–687. <https://doi.org/10.1038/nn870>.
- 617 16. Gosselin, F., and Schyns, P.G. (2001). Bubbles: a technique to reveal the use of information in
618 recognition tasks. *Vision Res.* 41, 2261–2271. [https://doi.org/10.1016/S0042-6989\(01\)00097-9](https://doi.org/10.1016/S0042-6989(01)00097-9).

- 619 17. Nielsen, K.J., Logothetis, N.K., and Rainer, G. (2006). Discrimination Strategies of Humans and
620 Rhesus Monkeys for Complex Visual Displays. *Curr. Biol.* *16*, 814–820.
621 <https://doi.org/10.1016/j.cub.2006.03.027>.
- 622 18. Gibson, B.M., Lazareva, O.F., Gosselin, F., Schyns, P.G., and Wasserman, E.A. (2007).
623 Nonaccidental Properties Underlie Shape Recognition in Mammalian and Nonmammalian Vision.
624 *Curr. Biol.* *17*, 336–340. <https://doi.org/10.1016/j.cub.2006.12.025>.
- 625 19. Kollmorgen, S., Nortmann, N., Schröder, S., and König, P. (2010). Influence of Low-Level
626 Stimulus Features, Task Dependent Factors, and Spatial Biases on Overt Visual Attention. *PLoS*
627 *Comput. Biol.* *6*, e1000791. <https://doi.org/10.1371/journal.pcbi.1000791>.
- 628 20. Tang, H., Buia, C., Madhavan, R., Crone, N.E., Madsen, J.R., Anderson, W.S., and Kreiman, G.
629 (2014). Spatiotemporal dynamics underlying object completion in human ventral visual cortex.
630 *Neuron* *83*, 736–748. <https://doi.org/10.1016/j.neuron.2014.06.017>.
- 631 21. Nielsen, K.J., Logothetis, N.K., and Rainer, G. (2006). Dissociation Between Local Field
632 Potentials and Spiking Activity in Macaque Inferior Temporal Cortex Reveals Diagnosticity-
633 Based Encoding of Complex Objects. *J. Neurosci.* *26*, 9639–9645.
634 <https://doi.org/10.1523/JNEUROSCI.2273-06.2006>.
- 635 22. Snodgrass, J.G., and Corwin, J. (1988). Perceptual Identification Thresholds for 150 Fragmented
636 Pictures from the Snodgrass and Vanderwart Picture Set. *Percept. Mot. Skills* *67*, 3–36.
637 <https://doi.org/10.2466/pms.1988.67.1.3>.
- 638 23. Gruber, T., Trujillo-Barreto, N.J., Giabbiconi, C.-M., Valdés-Sosa, P.A., and Müller, M.M.
639 (2006). Brain electrical tomography (BET) analysis of induced gamma band responses during a
640 simple object recognition task. *Neuroimage* *29*, 888–900.
641 <https://doi.org/10.1016/j.neuroimage.2005.09.004>.
- 642 24. Grutzner, C., Uhlhaas, P.J., Genc, E., Kohler, A., Singer, W., and Wibrall, M. (2010).
643 Neuroelectromagnetic Correlates of Perceptual Closure Processes. *J. Neurosci.* *30*, 8342–8352.
644 <https://doi.org/10.1523/JNEUROSCI.5434-09.2010>.
- 645 25. Tallon-Baudry, C., and Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in
646 object representation. *Trends Cogn. Sci.* *3*, 151–162. [https://doi.org/10.1016/S1364-6613\(99\)01299-1](https://doi.org/10.1016/S1364-6613(99)01299-1).
- 648 26. Ullman, S., Assif, L., Fetaya, E., and Harari, D. (2016). Atoms of recognition in human and
649 computer vision. *Proc. Natl. Acad. Sci. USA* *113*, 2744–2749.
650 <https://doi.org/10.1073/pnas.1513198113>.
- 651 27. Srivastava, S., Ben-Yosef, G., and Boix, X. (2019). Minimal images in deep neural networks:
652 Fragile object recognition in natural images. In 7th International Conference on Learning
653 Representations (ICLR 2019).
- 654 28. VanRullen, R. (2011). Four common conceptual fallacies in mapping the time course of
655 recognition. *Front. Psychol.* *2*, 1–6. <https://doi.org/10.3389/fpsyg.2011.00365>.
- 656 29. Liu, H., Agam, Y., Madsen, J.R., and Kreiman, G. (2009). Timing, timing, timing: Fast decoding
657 of object information from intracranial field potentials in human visual cortex. *Neuron* *62*, 281–
658 290. <https://doi.org/10.1016/j.neuron.2009.02.025>.
- 659 30. Hartigan, J.A., and Hartigan, P.M. (1985). The Dip Test of Unimodality. *Ann. Stat.* *13*, 1403–
660 1433. <https://doi.org/10.1214/aos/1176346577>.

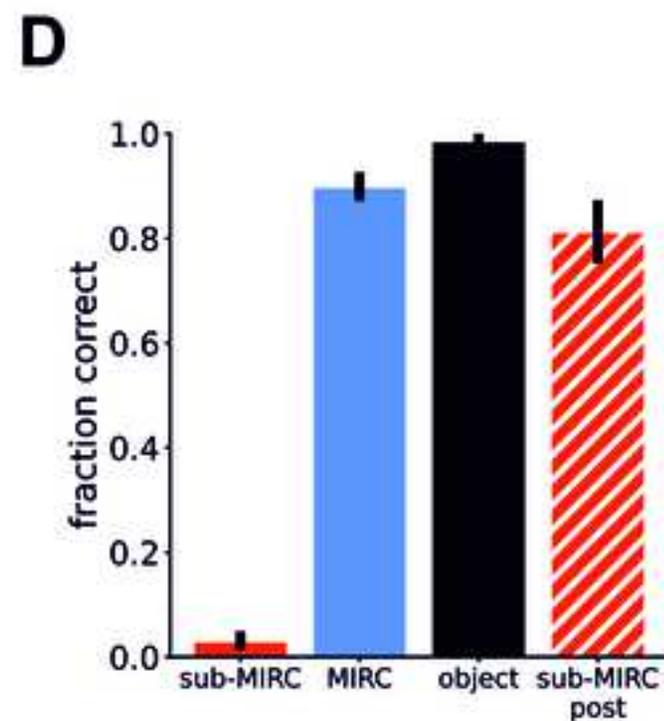
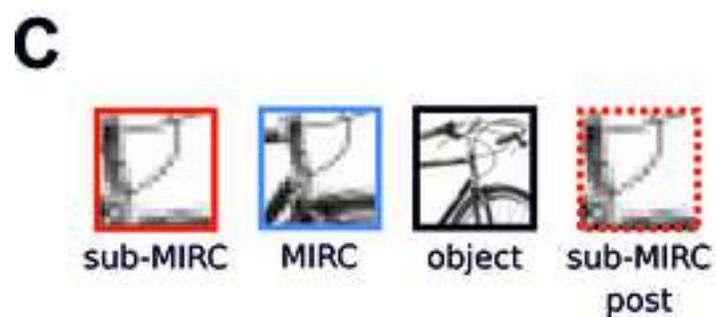
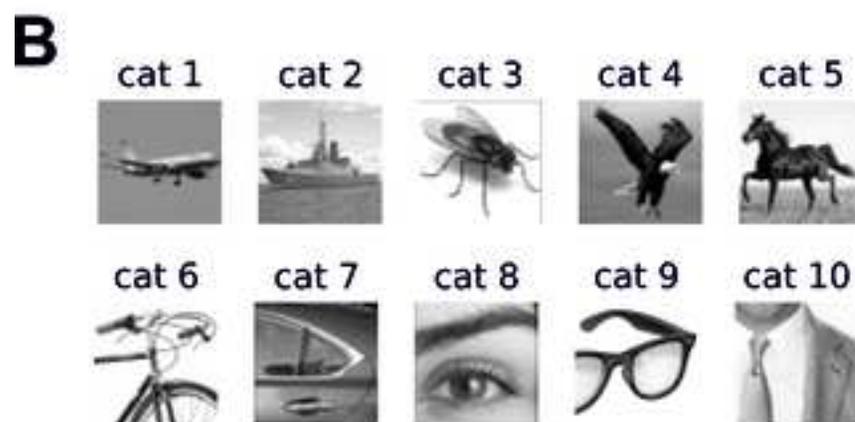
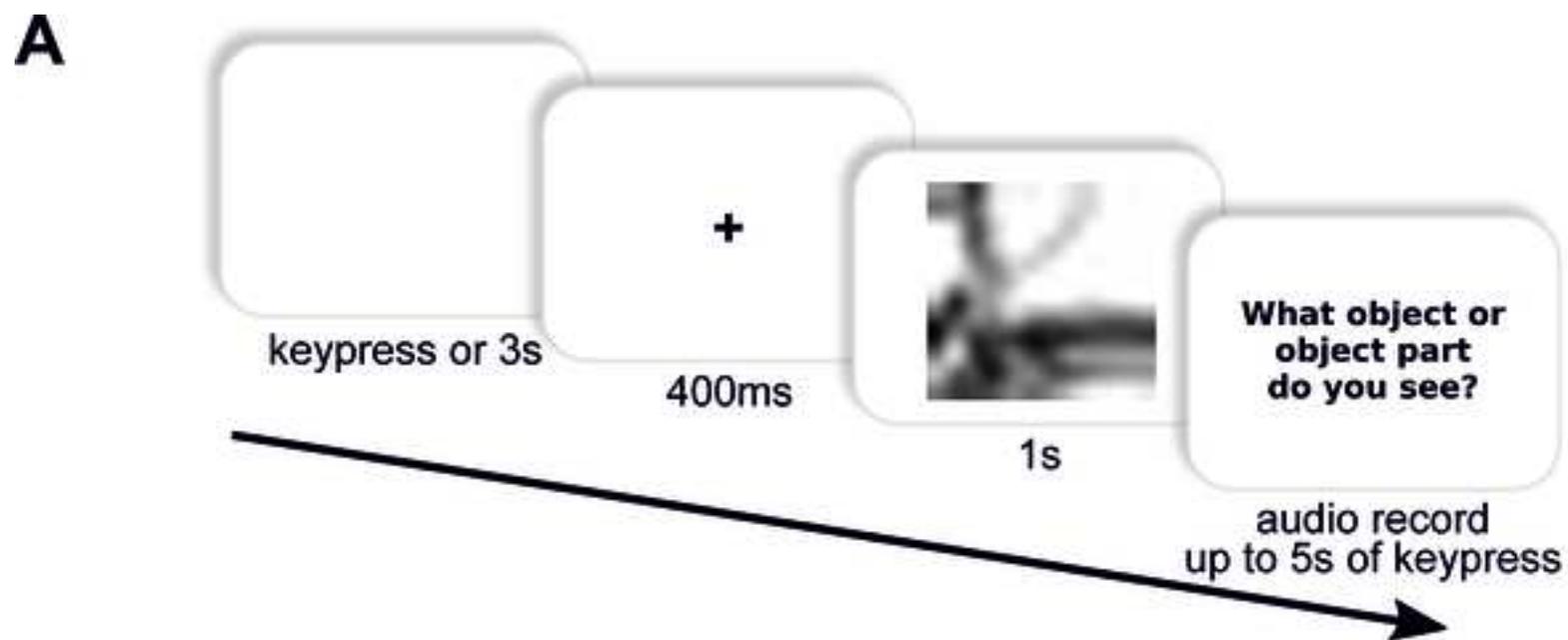
- 661 31. Baccalá, L.A., Sameshima, K., and Takahashi, D.Y. (2007). Generalized Partial Directed
662 Coherence. In 2007 15th International Conference on Digital Signal Processing (IEEE), pp. 163–
663 166. <https://doi.org/10.1109/ICDSP.2007.4288544>.
- 664 32. Baccalá, L.A., and Sameshima, K. (2001). Partial directed coherence: a new concept in neural
665 structure determination. *Biol. Cybern.* *84*, 463–474. <https://doi.org/10.1007/PL00007990>.
- 666 33. Schall, J.D. (2015). Visuomotor Functions in the Frontal Lobe. *Annu. Rev. Vis. Sci.* *1*, 469–498.
667 <https://doi.org/10.1146/annurev-vision-082114-035317>.
- 668 34. Wilson, F.A.W., Scalaidhe, S.P.Ó., and Goldman-Rakic, P.S. (1993). Dissociation of Object and
669 Spatial Processing Domains in Primate Prefrontal Cortex. *Science (80-.)*. *260*, 1955–1958.
670 <https://doi.org/10.1126/science.8316836>.
- 671 35. Meyer, T., Qi, X.-L., Stanford, T.R., and Constantinidis, C. (2011). Stimulus Selectivity in Dorsal
672 and Ventral Prefrontal Cortex after Training in Working Memory Tasks. *J. Neurosci.* *31*, 6266–
673 6276. <https://doi.org/10.1523/JNEUROSCI.6798-10.2011>.
- 674 36. Ó Scalaidhe, S.P., Wilson, F.A.W., and Goldman-Rakic, P.S. (1997). Areal segregation of face-
675 processing neurons in prefrontal cortex. *Science (80-.)*. *278*, 1135–1138.
676 <https://doi.org/10.1126/science.278.5340.1135>.
- 677 37. Rainer, G., and Ranganath, C. (2002). Coding of objects in the prefrontal cortex in monkeys and
678 humans. *Neuroscientist* *8*, 6–11. <https://doi.org/10.1177/107385840200800104>.
- 679 38. Rainer, G., and Miller, E.K. (2000). Effects of visual experience on the representation of objects in
680 the prefrontal cortex. *Neuron* *27*, 179–189.
- 681 39. Meyers, E.M., Freedman, D.J., Kreiman, G., Miller, E.K., and Poggio, T. (2008). Dynamic
682 Population Coding of Category Information in Inferior Temporal and Prefrontal Cortex. *J.*
683 *Neurophysiol.* *100*, 1407–1419. <https://doi.org/10.1152/jn.90248.2008>.
- 684 40. Wutz, A., Loonis, R., Roy, J.E., Donoghue, J.A., and Miller, E.K. (2018). Different Levels of
685 Category Abstraction by Different Dynamics in Different Prefrontal Areas. *Neuron* *97*, 716-
686 726.e8. <https://doi.org/10.1016/j.neuron.2018.01.009>.
- 687 41. Martinovic, J., Gruber, T., Hantsch, A., and Müller, M.M. (2008). Induced gamma-band activity is
688 related to the time point of object identification. *Brain Res.* *1198*, 93–106.
689 <https://doi.org/10.1016/j.brainres.2007.12.050>.
- 690 42. Stuss, D.T., Picton, T.W., Cerri, A.M., Leech, E.E., and Stethem, L.. (1992). Perceptual closure
691 and object identification: Electrophysiological responses to incomplete pictures. *Brain Cogn.* *19*,
692 253–266. [https://doi.org/10.1016/0278-2626\(92\)90047-P](https://doi.org/10.1016/0278-2626(92)90047-P).
- 693 43. Bar, M., Kassam, K.S., Ghuman, A.S., Boshyan, J., Schmid, A.M., Dale, A.M., Hamalainen, M.S.,
694 Marinkovic, K., Schacter, D.L., Rosen, B.R., et al. (2006). Top-down facilitation of visual
695 recognition. *Proc. Natl. Acad. Sci.* *103*, 449–454. <https://doi.org/10.1073/pnas.0507062103>.
- 696 44. Fyall, A.M., El-Shamayleh, Y., Choi, H., Shea-Brown, E., and Pasupathy, A. (2017). Dynamic
697 representation of partially occluded objects in primate prefrontal and visual cortex. *Elife* *6*, 1–25.
698 <https://doi.org/10.7554/eLife.25784>.
- 699 45. Kar, K., and DiCarlo, J.J. (2021). Fast Recurrent Processing via Ventrolateral Prefrontal Cortex Is
700 Needed by the Primate Ventral Stream for Robust Core Visual Object Recognition. *Neuron* *109*,
701 164-176.e5. <https://doi.org/10.1016/j.neuron.2020.09.035>.

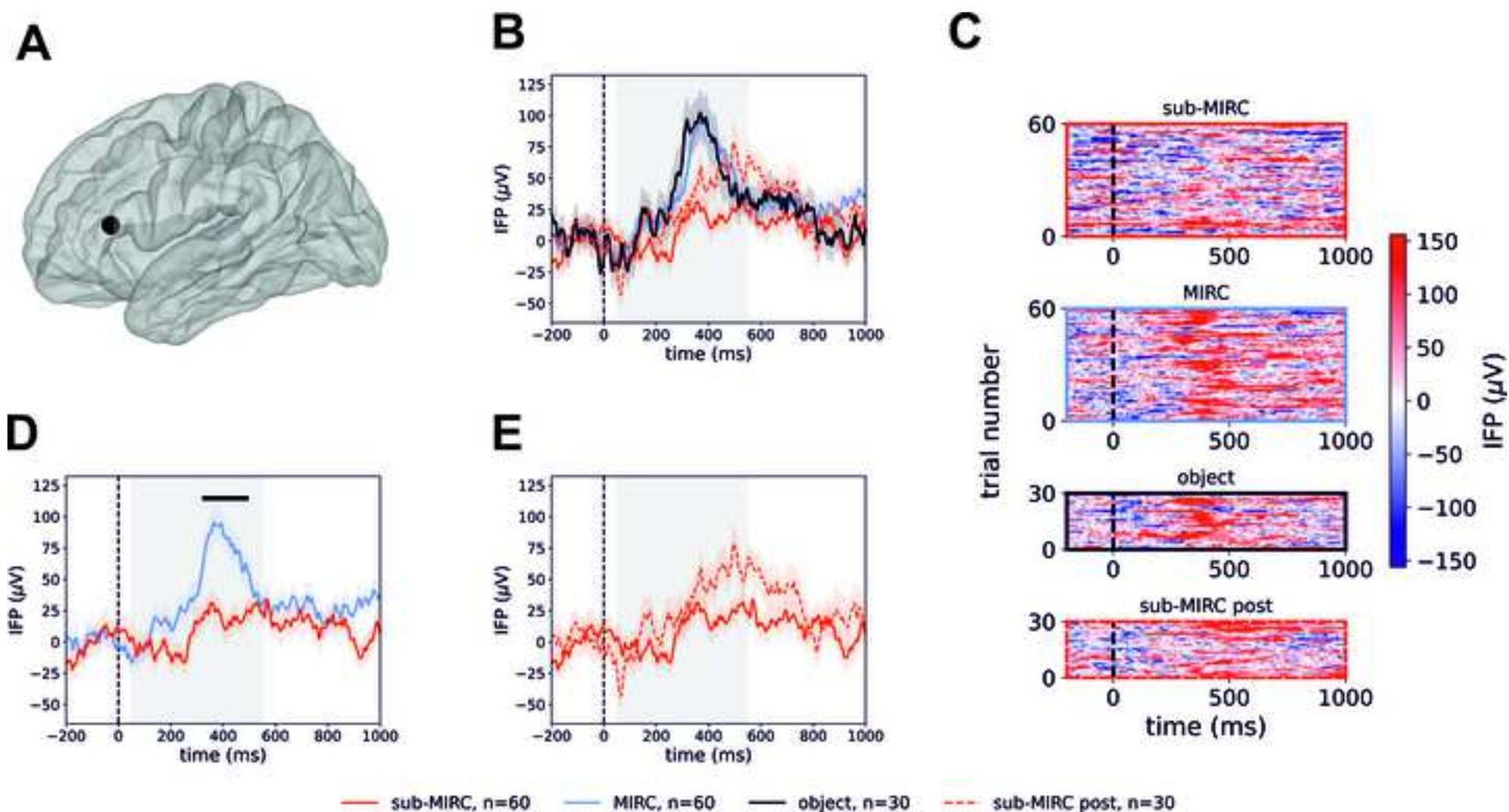
- 702 46. Romanski, L.M., and Chafee, M. V (2021). A View from the Top: Prefrontal Control of Object
703 Recognition. *Neuron* 109, 6–8. <https://doi.org/10.1016/j.neuron.2020.12.014>.
- 704 47. Seger, C.A., and Miller, E.K. (2010). Category Learning in the Brain. *Annu. Rev. Neurosci.* 33,
705 203–219. <https://doi.org/10.1146/annurev.neuro.051508.135546>.
- 706 48. Miller, E.K., Freedman, D.J., and Wallis, J.D. (2002). The prefrontal cortex: categories, concepts
707 and cognition. *Philos. Trans. R. Soc. London. Ser. B Biol. Sci.* 357, 1123–1136.
708 <https://doi.org/10.1098/rstb.2002.1099>.
- 709 49. Miller, E.K., Nieder, A., Freedman, D.J., and Wallis, J.D. (2003). Neural correlates of categories
710 and concepts. *Curr. Opin. Neurobiol.* 13, 198–203. [https://doi.org/10.1016/S0959-4388\(03\)00037-](https://doi.org/10.1016/S0959-4388(03)00037-0)
711 0.
- 712 50. Freedman, D.J., Riesenhuber, M., Poggio, T., and Miller, E.K. (2001). Categorical Representation
713 of Visual Stimuli in the Primate Prefrontal Cortex. *Science* (80-.). 291, 312–316.
714 <https://doi.org/10.1126/science.291.5502.312>.
- 715 51. Freedman, D.J., Riesenhuber, M., Poggio, T., and Miller, E.K. (2002). Visual Categorization and
716 the Primate Prefrontal Cortex: Neurophysiology and Behavior. *J. Neurophysiol.* 88, 929–941.
717 <https://doi.org/10.1152/jn.2002.88.2.929>.
- 718 52. Bertrand, J.-A., Tremblay, J., Lassonde, M., Vannasing, P., Khoa Nguyen, D., Robert, M.,
719 Bouthillier, A., and Lepore, F. (2013). Induced gamma-band response to fragmented images: An
720 intracranial EEG study. *Neuropsychologia* 51, 584–591.
721 <https://doi.org/10.1016/j.neuropsychologia.2013.01.002>.
- 722 53. Gruber, L.Z., Ullman, S., and Ahissar, E. (2021). Oculo-retinal dynamics can explain the
723 perception of minimal recognizable configurations. *Proc. Natl. Acad. Sci. U. S. A.* 118,
724 e2022792118. <https://doi.org/10.1073/pnas.2022792118>.
- 725 54. Chao, Z.C., Takaura, K., Wang, L., Fujii, N., and Dehaene, S. (2018). large-scale cortical
726 networks for hierarchical prediction and prediction error in the primate brain. *Neuron* 100, 1252-
727 1266.e3. <https://doi.org/10.2139/ssrn.3188377>.
- 728 55. Jensen, O., Bonnefond, M., Marshall, T.R., and Tiesinga, P. (2015). Oscillatory mechanisms of
729 feedforward and feedback visual processing. *Trends Neurosci.* 38, 192–194.
730 <https://doi.org/10.1016/j.tins.2015.02.006>.
- 731 56. Parto-Dezfouli, M., Vezoli, J., Bosman, C.A., and Fries, P. (2023). Enhanced behavioral
732 performance through interareal gamma and beta synchronization. *Cell Rep.* 42, 113249.
733 <https://doi.org/10.1016/j.celrep.2023.113249>.
- 734 57. Bastos, A.M., Vezoli, J., Bosman, C.A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J.R., De
735 Weerd, P., Kennedy, H., and Fries, P. (2015). Visual areas exert feedforward and feedback
736 influences through distinct frequency channels. *Neuron* 85, 390–401.
737 <https://doi.org/10.1016/j.neuron.2014.12.018>.
- 738 58. Loh, K.K., Petrides, M., Hopkins, W.D., Procyk, E., and Amiez, C. (2017). Cognitive control of
739 vocalizations in the primate ventrolateral-dorsomedial frontal (VLF-DMF) brain network.
740 *Neurosci. Biobehav. Rev.* 82, 32–44. <https://doi.org/10.1016/j.neubiorev.2016.12.001>.
- 741 59. Doniger, G.M., Foxe, J.J., Murray, M.M., Higgins, B.A., Snodgrass, J.G., Schroeder, C.E., and
742 Javitt, D.C. (2000). Activation Timecourse of Ventral Visual Stream Object-recognition Areas:
743 High Density Electrical Mapping of Perceptual Closure Processes. *J. Cogn. Neurosci.* 12, 615–
744 621. <https://doi.org/10.1162/089892900562372>.

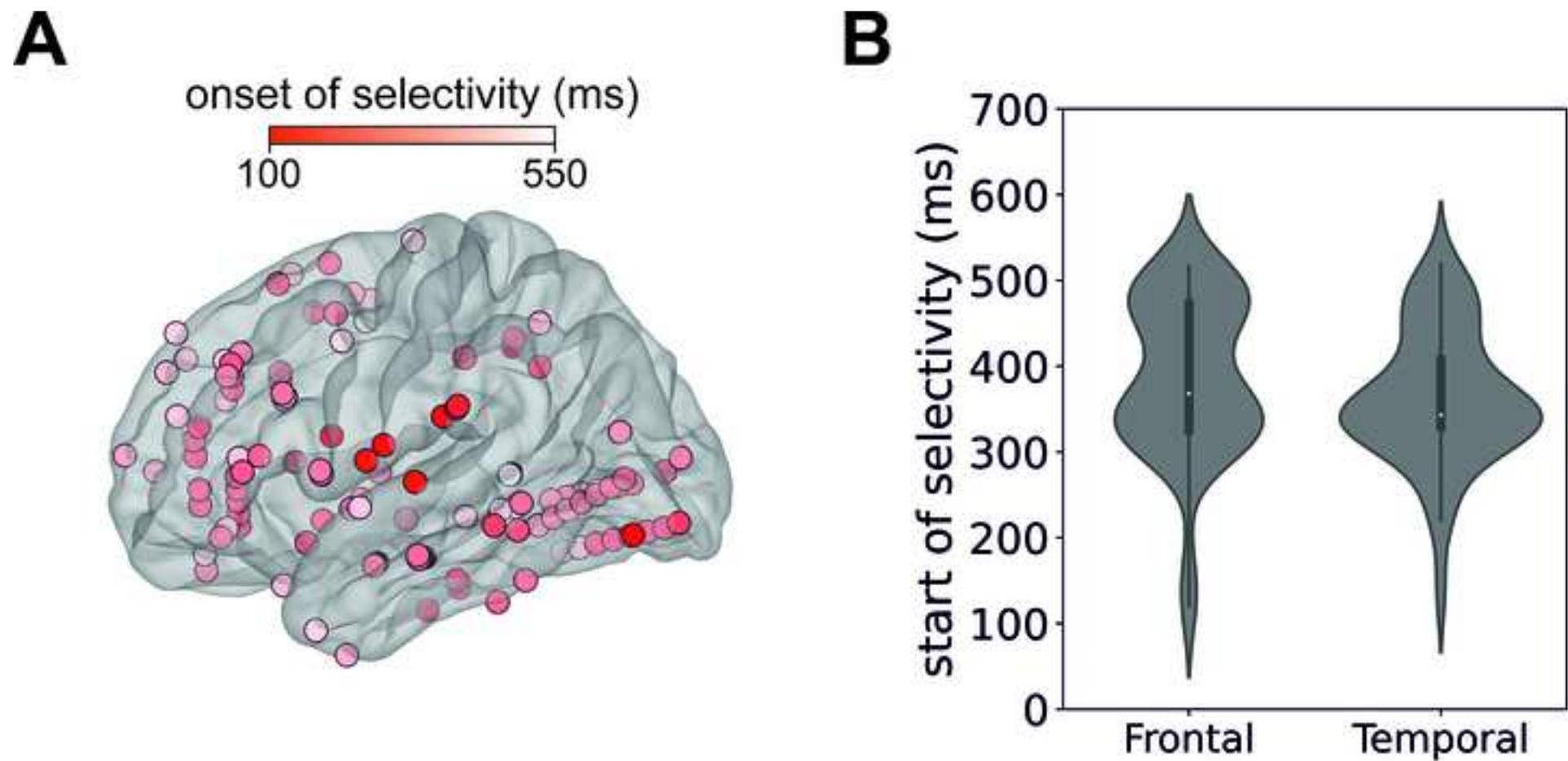
- 745 60. Sehatpour, P., Molholm, S., Schwartz, T.H., Mahoney, J.R., Mehta, A.D., Javitt, D.C., Stanton,
746 P.K., and Foxe, J.J. (2008). A human intracranial study of long-range oscillatory coherence across
747 a frontal-occipital-hippocampal brain network during visual object processing. *Proc. Natl. Acad.*
748 *Sci. U. S. A. 105*, 4399–4404. <https://doi.org/10.1073/pnas.0708418105>.
- 749 61. Gruber, T., Maess, B., Trujillo-Barreto, N.J., and Müller, M.M. (2008). Sources of synchronized
750 induced Gamma-Band responses during a simple object recognition task: A replication study in
751 human MEG. *Brain Res. 1196*, 74–84. <https://doi.org/10.1016/j.brainres.2007.12.037>.
- 752 62. Namima, T., and Pasupathy, A. (2021). Encoding of partially occluded and occluding objects in
753 primate inferior temporal cortex. *J. Neurosci. 41*, 5662–5666.
754 <https://doi.org/10.1523/JNEUROSCI.2992-20.2021>.
- 755 63. Kosai, Y., El-Shamayleh, Y., Fyall, A.M., and Pasupathy, A. (2014). The role of visual area V4 in
756 the discrimination of partially occluded shapes. *J. Neurosci. 34*, 8570–8584.
757 <https://doi.org/10.1523/JNEUROSCI.1375-14.2014>.
- 758 64. Kovács, G., Vogels, R., and Orban, G.A. (1995). Selectivity of macaque inferior temporal neurons
759 for partially occluded shapes. *J. Neurosci. 15*, 1984–1997. [https://doi.org/10.1523/jneurosci.15-03-](https://doi.org/10.1523/jneurosci.15-03-01984.1995)
760 [01984.1995](https://doi.org/10.1523/jneurosci.15-03-01984.1995).
- 761 65. Holzinger, Y., Ullman, S., Harari, D., Behrmann, M., and Avidan, G. (2019). Minimal
762 recognizable configurations elicit category-selective responses in higher order visual cortex. *J.*
763 *Cogn. Neurosci. 31*, 1354–1367. https://doi.org/10.1162/jocn_a_01420.
- 764 66. Tovee, M.J., Rolls, E.T., and Ramachandran, V.S. (1996). Rapid visual learning in neurones of the
765 primate temporal visual cortex. *Neuroreport 7*, 2757–2760. [https://doi.org/10.1097/00001756-](https://doi.org/10.1097/00001756-199611040-00070)
766 [199611040-00070](https://doi.org/10.1097/00001756-199611040-00070).
- 767 67. Chalupa, L.M., and Werner, J.S. (2003). *The visual neurosciences* (Bradford).
- 768 68. Hung, C.P., Kreiman, G., Poggio, T., and DiCarlo, J.J. (2005). Fast readout of object identity from
769 macaque inferior temporal cortex. *Science (80-.). 310*, 863–866.
770 <https://doi.org/10.1126/science.1117593>.
- 771 69. Thorpe, S., Fize, D., and Marlot, C. (1996). Speed of processing in the human visual system.
772 *Nature 381*, 520–522. <https://doi.org/10.1038/381520a0>.
- 773 70. Harari, D., Benoni, H., and Ullman, S. (2020). Object recognition at the level of minimal images
774 develops for up to seconds of presentation time. *J. Vis. 20*, 266.
775 <https://doi.org/10.1167/jov.20.11.266>.
- 776 71. Tang, H., Schrimpf, M., Lotter, W., Moerman, C., Paredes, A., Caro, J.O., Hardesty, W., Cox, D.,
777 and Kreiman, G. (2018). Recurrent computations for visual pattern completion. *Proc. Natl. Acad.*
778 *Sci. USA 115*, 8835–8840. <https://doi.org/10.1073/pnas.1719397115>.
- 779 72. Quiroga, R.Q., Reddy, L., Kreiman, G., Koch, C., and Fried, I. (2005). Invariant visual
780 representation by single neurons in the human brain. *Nature 435*, 1102–1107.
781 <https://doi.org/10.1038/nature03687>.
- 782 73. Mormann, F., Kornblith, S., Quiroga, R.Q., Kraskov, A., Cerf, M., Fried, I., and Koch, C. (2008).
783 Latency and Selectivity of Single Neurons Indicate Hierarchical Processing in the Human Medial
784 Temporal Lobe. *J. Neurosci. 28*, 8865–8872. <https://doi.org/10.1523/JNEUROSCI.1640-08.2008>.
- 785 74. Rey, H.G., Fried, I., and Quiroga, R. (2014). Timing of Single-Neuron and Local Field
786 Potential Responses in the Human Medial Temporal Lobe. *Curr. Biol. 24*, 299–304.

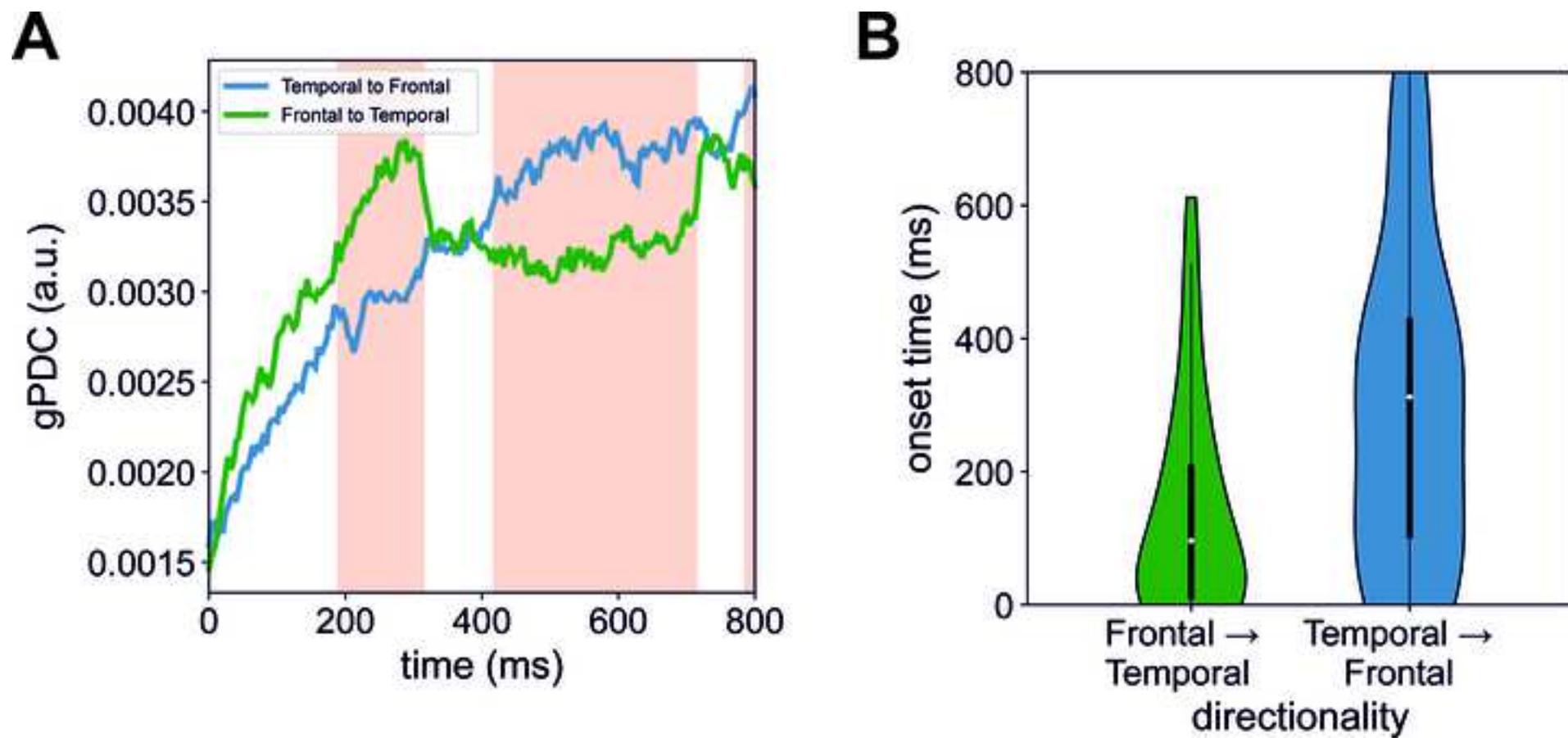
- 787 <https://doi.org/10.1016/j.cub.2013.12.004>.
- 788 75. Quiroga, R.Q., Mukame, R., Isham, E.A., Malach, R., and Fried, I. (2008). Human single-neuron
789 responses at the threshold of conscious recognition. *Proc. Natl. Acad. Sci. U. S. A.* *105*, 3599–
790 3604. <https://doi.org/10.1073/pnas.0707043105>.
- 791 76. Bova, S.M., Fazzi, E., Giovenzana, A., Montomoli, C., Signorini, S.G., Zoppello, M., and Lanzi,
792 G. (2007). The Development of Visual Object Recognition in School-Age Children. *Dev.*
793 *Neuropsychol.* *31*, 79–102. https://doi.org/10.1207/s15326942dn3101_5.
- 794 77. Huber, L.S., Geirhos, R., and Wichmann, F.A. (2023). The developmental trajectory of object
795 recognition robustness: Children are like small adults but unlike big deep neural networks. *J. Vis.*
796 *23*, 1–30. <https://doi.org/10.1167/jov.23.7.4>.
- 797 78. Fukushima, K. (1980). Neocognitron: A self-organizing neural network model for a mechanism of
798 pattern recognition unaffected by shift in position. *Biol. Cybern.* *36*, 193–202.
799 <https://doi.org/10.1007/BF00344251>.
- 800 79. Riesenhuber, M., and Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nat.*
801 *Neurosci.* *2*, 1019–1025. <https://doi.org/10.1038/14819>.
- 802 80. Krizhevsky, A., Sutskever, I., and Hinton, G.E. (2012). ImageNet classification with deep
803 convolutional neural networks. In *Advances in Neural Information Processing Systems 25 (NIPS*
804 *2012)*.
- 805 81. Krizhevsky, A., Sutskever, I., and Hinton, G.E. (2017). ImageNet classification with deep
806 convolutional neural networks. *Commun. ACM* *60*, 84–90. <https://doi.org/10.1145/3065386>.
- 807 82. Rajalingham, R., Issa, E.B., Bashivan, P., Kar, K., Schmidt, K., and DiCarlo, J.J. (2018). Large-
808 scale, high-resolution comparison of the core visual object recognition behavior of humans,
809 monkeys, and state-of-the-art deep artificial neural networks. *J. Neurosci.* *38*, 7255–7269.
810 <https://doi.org/10.1523/JNEUROSCI.0388-18.2018>.
- 811 83. Yamins, D.L.K., Hong, H., Cadieu, C.F., Solomon, E.A., Seibert, D., and Dicarlo, J.J. (2014).
812 Performance-optimized hierarchical models predict neural responses in higher visual cortex. *Proc.*
813 *Natl. Acad. Sci. U. S. A.* <https://doi.org/10.1073/pnas.1403112111>.
- 814 84. Serre, T. (2019). Deep Learning: The Good, the Bad, and the Ugly. *Annu. Rev. Vis. Sci.* *5*, 399–
815 426. <https://doi.org/10.1146/annurev-vision-091718-014951>.
- 816 85. Kreiman, G., and Serre, T. (2020). Beyond the feedforward sweep: feedback computations in the
817 visual cortex. *Ann. N. Y. Acad. Sci.* *1464*, 222–241. <https://doi.org/10.1111/nyas.14320>.
- 818 86. Dale, A.M., Fischl, B., and Sereno, M.I. (1999). Cortical Surface-Based Analysis. *Neuroimage* *9*,
819 179–194. <https://doi.org/10.1006/nimg.1998.0395>.
- 820 87. Groppe, D.M., Bickel, S., Dykstra, A.R., Wang, X., Mégevand, P., Mercier, M.R., Lado, F.A.,
821 Mehta, A.D., and Honey, C.J. (2017). iELVis: An open source MATLAB toolbox for localizing
822 and visualizing human intracranial electrode data. *J. Neurosci. Methods* *281*, 40–48.
823 <https://doi.org/10.1016/j.jneumeth.2017.01.022>.
- 824 88. Ojemann, G.A. (1997). Treatment of temporal lobe epilepsy. *Annu. Rev. Med.* *48*, 317–328.
825 <https://doi.org/10.1146/annurev.med.48.1.317>.
- 826 89. Destrieux, C., Fischl, B., Dale, A., and Halgren, E. (2010). Automatic parcellation of human
827 cortical gyri and sulci using standard anatomical nomenclature. *Neuroimage* *53*, 1–15.

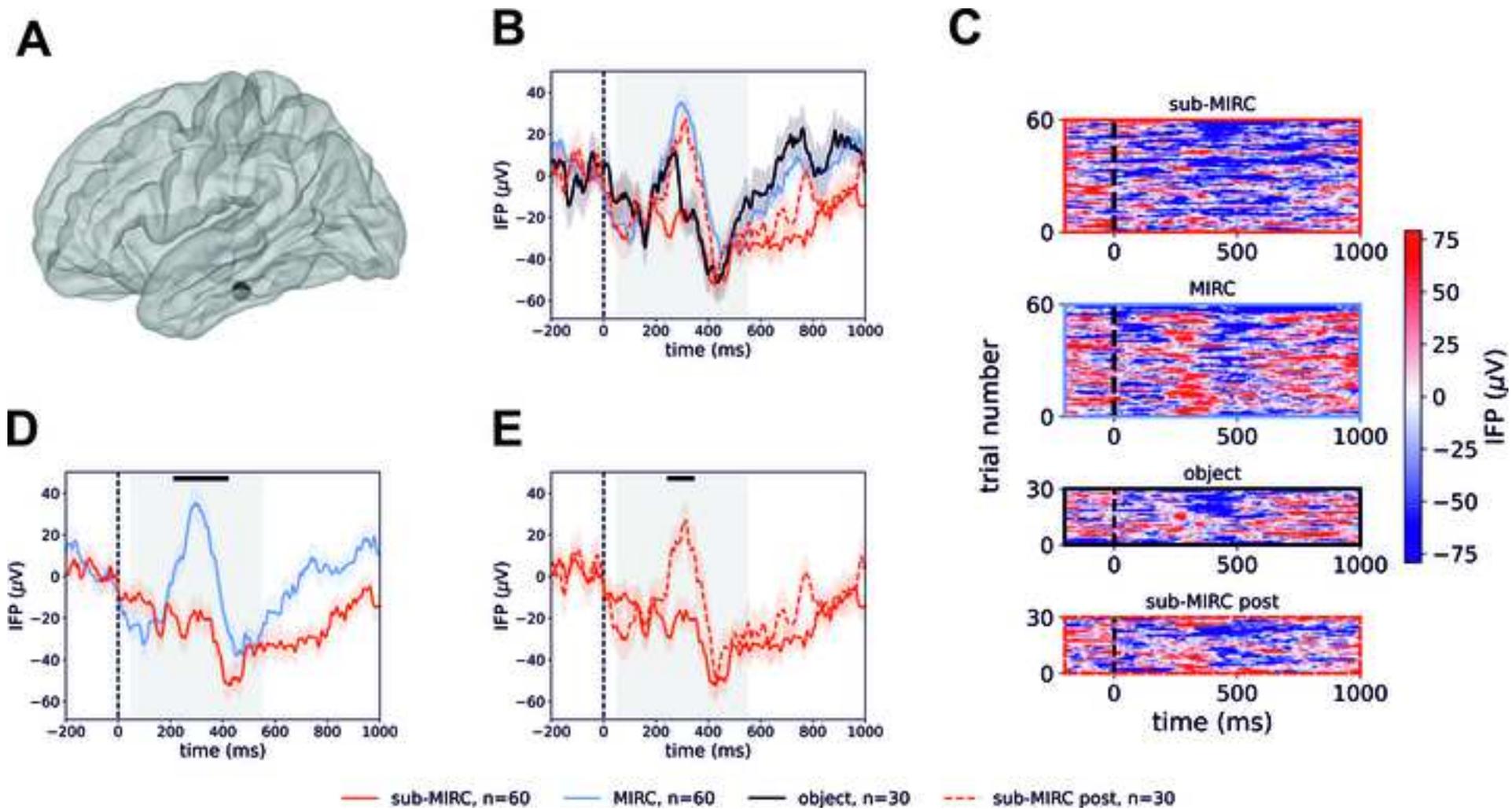
- 828 <https://doi.org/10.1016/j.neuroimage.2010.06.010>.
- 829 90. Dykstra, A.R., Chan, A.M., Quinn, B.T., Zepeda, R., Keller, C.J., Cormier, J., Madsen, J.R.,
830 Eskandar, E.N., and Cash, S.S. (2012). Individualized localization and cortical surface-based
831 registration of intracranial electrodes. *Neuroimage* 59, 3563–3570.
832 <https://doi.org/10.1016/j.neuroimage.2011.11.046>.
- 833 91. Geweke, J. (1982). Measurement of Linear Dependence and Feedback between Multiple Time
834 Series. *J. Am. Stat. Assoc.* 77, 304–313. <https://doi.org/10.1080/01621459.1982.10477803>.
- 835 92. Granger, C.W.J. (1969). Investigating causal relations by econometric models and cross-spectral
836 methods. *Econometrica* 37, 424–438.
- 837 93. Kamiński, M., Ding, M., Truccolo, W.A., and Bressler, S.L. (2001). Evaluating causal relations in
838 neural systems: Granger causality, directed transfer function and statistical assessment of
839 significance. *Biol. Cybern.* 85, 145–157. <https://doi.org/10.1007/s004220000235>.
- 840 94. Wen, X., Rangarajan, G., and Ding, M. (2013). Is Granger causality a viable technique for
841 analyzing fMRI data? *PLoS One* 8, e67428. <https://doi.org/10.1371/journal.pone.0067428>.
- 842 95. Gürkan, G., Akan, A., and Seyhan, T.Ö. (2014). Analysis of brain connectivity changes after
843 propofol injection by generalized partial directed coherence. *Digit. Signal Process.* 25, 156–163.
844 <https://doi.org/10.1016/j.dsp.2013.11.011>.
- 845 96. Taxidis, J., Coomber, B., Mason, R., and Owen, M. (2010). Assessing cortico-hippocampal
846 functional connectivity under anesthesia and kainic acid using generalized partial directed
847 coherence. *Biol. Cybern.* 102, 327–340. <https://doi.org/10.1007/s00422-010-0370-1>.
- 848 97. Cometa, A., D’Orio, P., Revay, M., Micera, S., and Artoni, F. (2021). Stimulus evoked causality
849 estimation in stereo-EEG. *J. Neural Eng.* 18, 056041. <https://doi.org/10.1088/1741-2552/ac27fb>.
- 850 98. Ghumare, E.G., Schrooten, M., Vandenberghe, R., and Dupont, P. (2018). A time-varying
851 connectivity analysis from distributed EEG sources: A simulation study. *Brain Topogr.* 31, 721–
852 737. <https://doi.org/10.1007/s10548-018-0621-3>.
- 853 99. Milde, T., Leistriz, L., Astolfi, L., Miltner, W.H.R., Weiss, T., Babiloni, F., and Witte, H. (2010).
854 A new Kalman filter approach for the estimation of high-dimensional time-variant multivariate
855 AR models and its application in analysis of laser-evoked brain potentials. *Neuroimage* 50, 960–
856 969. <https://doi.org/10.1016/j.neuroimage.2009.12.110>.
- 857 100. Pagnotta, M.F., and Plomp, G. (2018). Time-varying MVAR algorithms for directed connectivity
858 analysis: Critical comparison in simulations and benchmark EEG data. *PLoS One* 13, e0198846.
859 <https://doi.org/10.1371/journal.pone.0198846>.
- 860 101. Florin, E., Gross, J., Pfeifer, J., Fink, G.R., and Timmermann, L. (2010). The effect of filtering on
861 Granger causality based multivariate causality measures. *Neuroimage* 50, 577–588.
862 <https://doi.org/10.1016/j.neuroimage.2009.12.050>.
- 863 102. Nichols, T., and Holmes, A. (2004). Nonparametric Permutation Tests for Functional
864 Neuroimaging. In *Human Brain Function* (Elsevier), pp. 887–910. <https://doi.org/10.1016/B978-012264841-0/50048-2>.

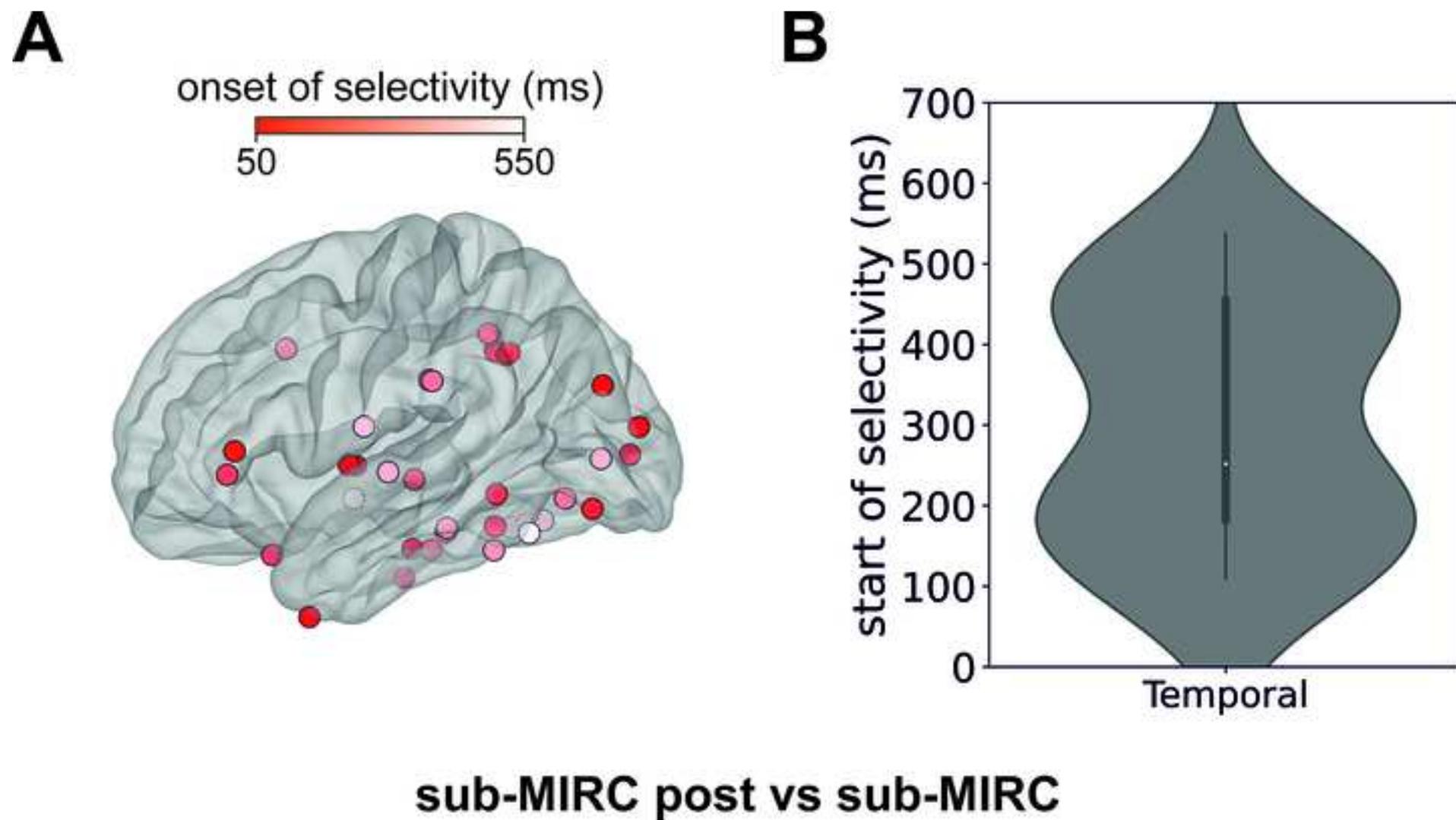












Casile *et al*, Neural correlates of minimal recognizable configurations in the human brain

1 Supplementary Tables

Region name	# Electrodes	Average MNI coordinates
G_temporal_middle	112	-60.82 -28.94 -12.43
G_front_middle	94	-37.68 30.46 32.94
G_front_sup	93	-9.95 23.86 39.87
G_temp_sup-Lateral	93	-60.7 -14.49 -4.11
G_occipital_middle	83	-35.48 -70.6 19.95
G_temporal_inf	67	-49.2 -26.57 -27.32
G_front_inf-Opercular	56	-48.92 12.29 10.84
S_temporal_inf	53	-49.73 -31.02 -17.01
Pole_occipital	51	-38.39 -35.8 21.38
G_pariet_inf-Supramar	50	-59.07 -35.03 30.91
S_temporal_sup	48	-46.44 -31.35 -2.51
G_oc-temp_med-Parahip	47	-27.73 -19.02 -19.4
G_precentral	42	-53.13 -0.39 36.9
S_front_inf	37	-37.91 24.89 23.38
G_front_inf-Triangul	33	-49.65 30.37 5.42
G&S_subcentral	31	-60.54 -4.83 15.96
G_pariet_inf-Angular	30	-44.01 -59.68 31.56
G&S_occipital_inf	29	-44.26 -60.85 13.45
G_orbital	29	-30.64 29.09 -16.97
G_postcentral	29	-52.57 -18.91 49.71
S_front_sup	27	-27.75 21.35 39.98
G_insular_short	26	-37.45 6.43 -4.04
S_circular_insula_inf	26	-40.51 -7.9 -11.32
S_collat_transv_ant	26	-37.78 -18.28 -22.26
Pole_temporal	25	-35.45 4.53 -39.32
S_orbital-H_Shaped	23	-36.44 35.96 -9.55
G&S_cingul-Ant	21	-14.14 41.5 4.38
S_circular_insula_sup	20	-34.17 2.58 6.54
G_oc-temp_lat-fusifor	17	-35.92 -45.83 -20.19
G&S_cingul-Mid-Ant	15	-11.67 19.98 22.99
S_oc-temp_lat	15	-44.79 -28. -22.56
G_temp_sup-Plan_tempo	13	-56.33 -37.03 8.31
S_front_middle	13	-29.85 39.74 14.51
S_postcentral	13	-31.77 -37.65 46.61
G_rectus	12	-6.01 48.56 -24.35
G_temp_sup-Plan_polar	11	-35.26 2.91 -21.76
S_pericallosal	11	-14.76 -30.52 12.26
S_precentral-inf-part	11	-41.99 9.23 22.37
G&S_frontomargin	10	-35.82 56.54 -8.87
G_occipital_sup	10	-20.03 -29.79 38.33
Lat_Fis-post	10	-44.36 -31.54 9.66
G&S_cingul-Mid-Post	9	-6.15 -20.08 35.88
G_oc-temp_med-Lingual	8	-10.37 -75.97 -8.28
G_precuneus	8	-2.76 -46.64 43.85
G_temp_sup-G_T_transv	8	-47.18 -13.58 9.09
S_intrapariet&P_trans	8	-36.38 -49.21 42.74
S_occipital_ant	7	-40.67 -66.72 -1.82
S_circular_insula_ant	6	-42.21 15.35 3.26
S_orbital_lateral	6	-53.85 32.58 13.59
G_Ins_lg&S_cent_ins	4	-34.72 1.59 -13.29
S_orbital_med-olfact	4	-10.49 38.35 -16.48
G&S_paracentral	3	-13.69 -42.52 62.77
G_parietal_sup	3	-36.53 -44.6 50.28
Lat_Fis-ant-Horizont	3	-32.23 33.54 -2.08
Lat_Fis-ant-Vertical	3	-46.15 20.54 12.04
S_oc-temp_med&Lingual	3	-34.48 -31.46 -15.18
S_suborbital	3	-12.17 44.2 -10.19
G&S_transv_frontopol	2	-9.95 68.48 -0.23
G_cuneus	2	-2.1 -82.47 11.71
G_front_inf-Orbital	2	-45.57 32.29 -15.75
S_collat_transv_post	2	-35.47 -82.49 -9.56
S_interm_prim-Jensen	2	-52.77 -52.5 28.19
S_calcarine	1	-10.39 -87.65 5.48
S_central	1	-24.11 -32.65 43.7
S_cingul-Marginalis	1	-5.2 -30.89 49.31
S_oc_middle&Lunatus	1	-28.2 -91.2 0.41
S_oc_sup&transversal	1	-19.77 -91.18 17.07
S_temporal_transverse	1	-50.2 -22.5 4.98

2 **Table S1 - Anatomical locations of all electrodes for which brain localization could be computed, Related**
3 **to STAR Methods.**

Participant #	Age	Gender	# Electrodes
1	17	M	229
2	25	M	190
3	18	F	83
4	15	F	212
5	35	F	125
6	26	F	104
7	12	M	96
8	43	F	181
9	22	F	122
10	11	F	158
11	21	M	94
12	12	M	158

Table S2 - Information about the 12 patients that participated in the study, Related to STAR Methods.

Participant #	Object	MIRC	subMI RC	subMI RC post
1	25	50	50	20
2	25	50	50	25
3	30	60	60	30
4	25	50	50	25
5	30	60	60	20
6	15	30	30	25
7	25	50	50	15
8	15	30	30	20
9	30	60	60	30
10	30	60	60	30
11	30	60	60	35
12	10	20	20	10

Table S3 - Number of trials that we considered in our analysis per condition for each participant, Related to STAR Methods.

6 Supplementary Figures

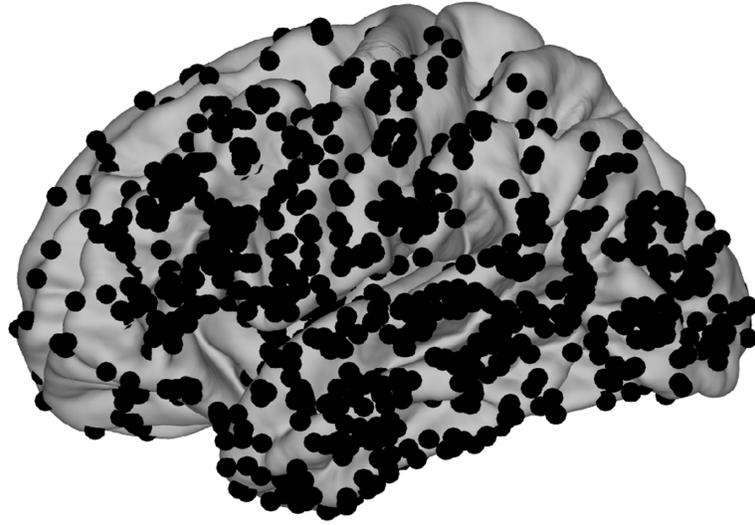


Figure S1 – Locations of recorded sites for which we could recover MNI coordinates across our cohort of patients (n=12, see also Table S1), Related to Figure 3, 6, and STAR Methods.

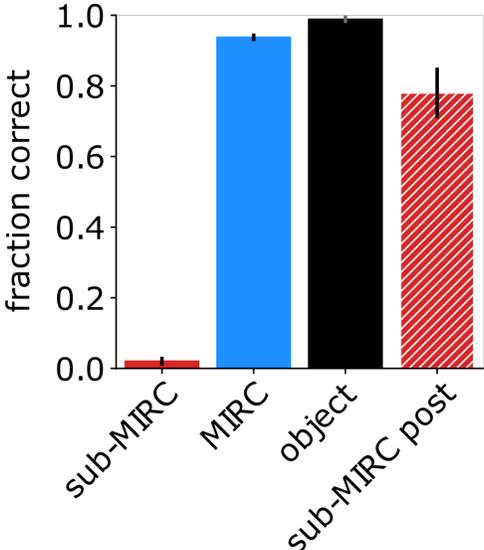


Figure S2 – Results of a behavioral study with 7 participants without epilepsy, Related to Figure 1 and STAR Methods. The format and conventions are as in Figure 1D.

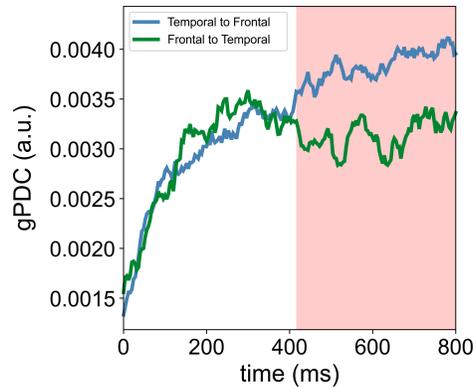


Figure S3 – Temporal dynamics of the functional interactions between temporal and frontal areas during the perception of sub-MIRC stimuli, Related to Figure 4. The panel shows the strength, as assessed by generalized Partial Directed Coherence (gPDC, Baccalá et al., 2007), of the temporal to frontal (green curve) and frontal to temporal (blue curve) functional interactions measured in participants ($n=6$) that had at least 2 responsive electrodes in both the temporal and frontal lobe. The curves represent the average gPDC obtained from $n=3639$ pairs of frontal and temporal electrodes respectively. Standard errors are shown but they are too small to be visible. Red-shaded areas mark intervals where the interactions in one direction are significantly stronger than in the opposite direction.

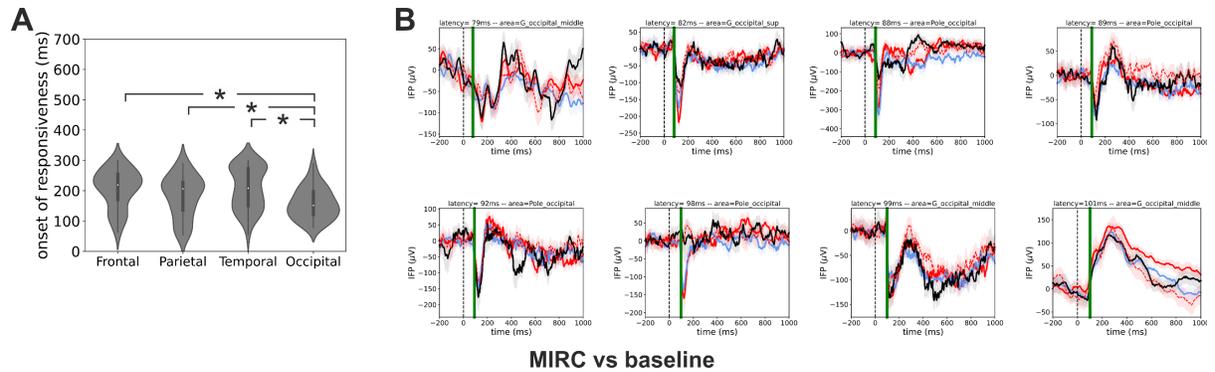


Figure S4 – Visual responses to MIRC stimuli, Related to Figures 2 and 3. (A) Distribution of responsivity start times for the MIRC stimuli in the occipital ($n=48$ electrodes, median=152ms), temporal ($n=78$, median=208ms), parietal ($n=47$, median=206ms) and frontal ($n=55$, median=219ms) lobes. We deemed visually responsive to MIRC stimuli those electrodes whose responses during MIRC trials were statistically different from baseline at a $p<0.01$ level (Wilcoxon ranksum test) for at least 50 consecutive time points (see Methods). Asterisks signify statistically different responses at the $p<0.05$ level. **(B)** Neural responses of the 8 MIRC-responsive electrodes with shortest latency located in the occipital lobe. The response latency and brain area of each electrode are shown in the title.

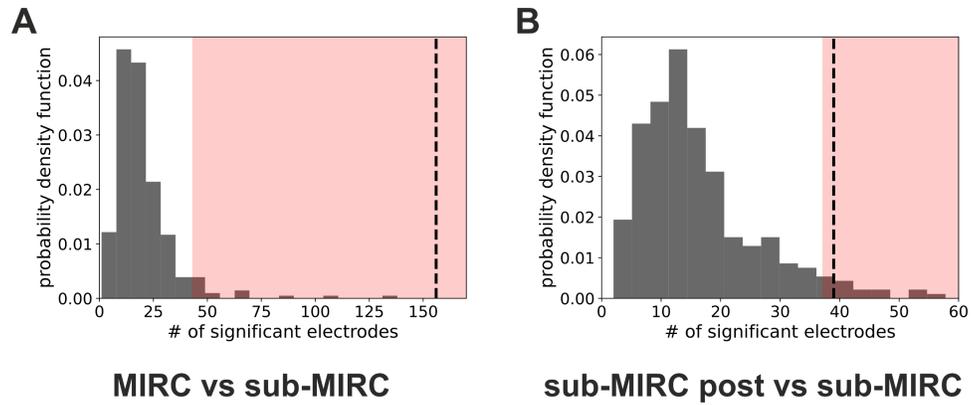


Figure S5 – Distributions of the False Discovery Rate (FDR) of the number of selective electrodes, Related to Figures 3, 6, and STAR Methods. The two panels show the distribution of the number of electrodes selective for MIRC versus sub-MIRC (A) and sub-MIRC post versus sub-MIRC (B) when the condition labels were randomly shuffled 500 times. In each panel, the red shaded area represents the top 5% tail of the distribution, and the vertical dotted line represents the number of selective electrodes found in the corresponding analysis (MIRC vs sub-MIRC: 156 electrodes, and sub-MIRC post vs sub-MIRC: 39 electrodes). In both cases our analyses have $FDR < 0.05$.

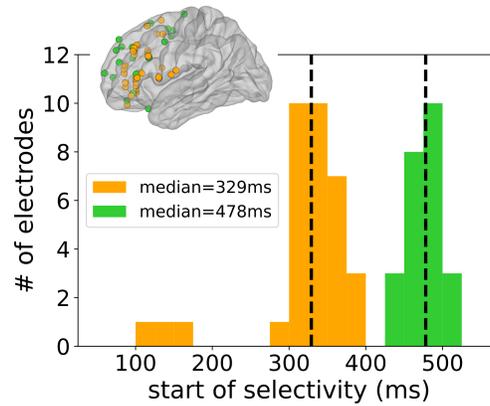


Figure S6 – Histograms of the selectivity start times of responses differentiating between MIRCs and sub-MIRCs in the frontal lobe, Related to Figure 3. The distribution was not unimodal (Hartigan’s dip test, $p < 0.005$) and it appeared to consist of two components: an “early” and a “late” component, color coded in orange and green, respectively. The legend shows the median of the two distributions and the inset the anatomical locations of the electrodes. The distribution of onset times contains data from 5 participants. At the single-participant level, due to sampling limitations, Hartigan’s dip test was significant in only one of our participants.

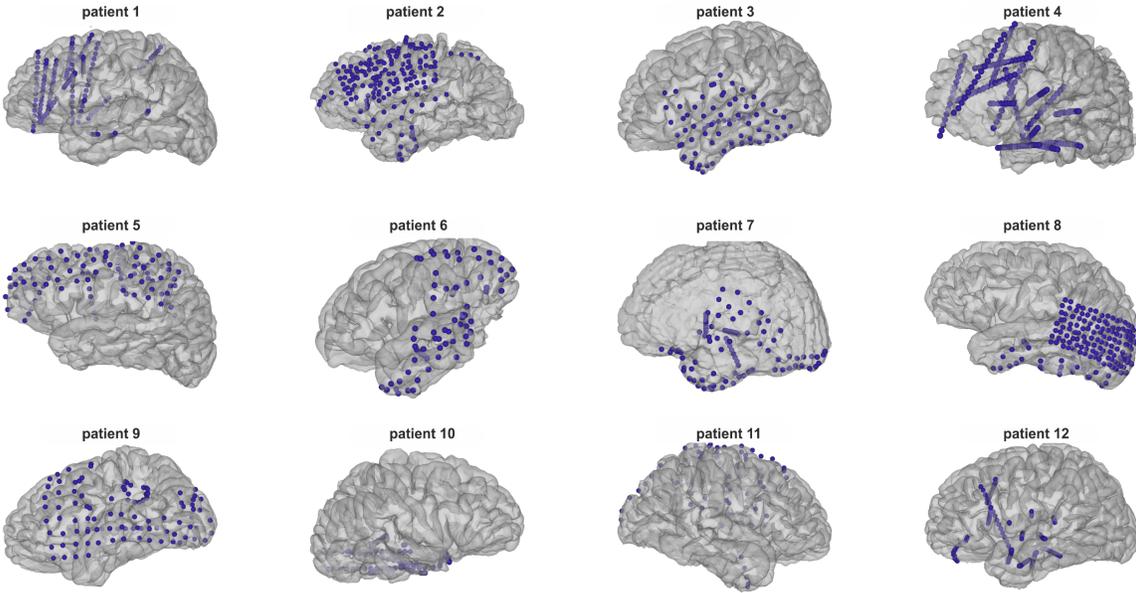


Figure S7 – Location of electrodes in each of the 12 participants, Related to STAR Methods.

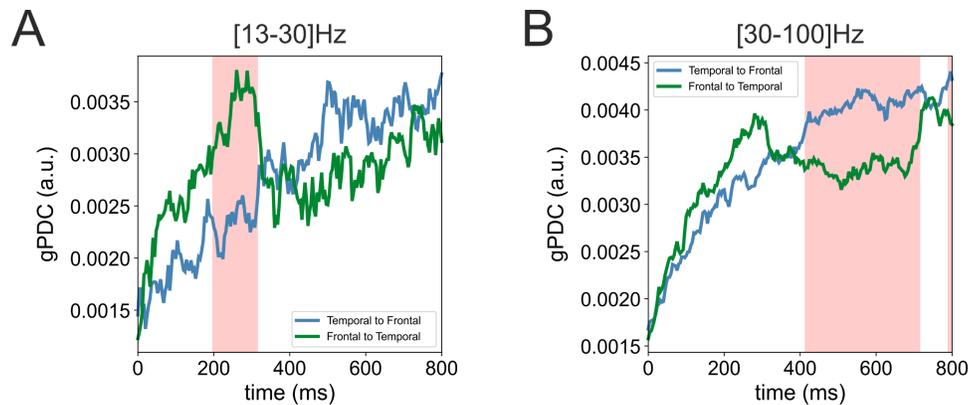


Figure S8 – Results of a frequency-resolved generalized Directed Partial Coherence (gDPC) analysis during the perception of MIRC stimuli, Related to Figure 4 and Discussion. The two panels show the strength, as assessed by generalized Partial Directed Coherence (gPDC, Baccalá *et al.*, 2007), of the temporal to frontal (blue curve) and frontal to temporal (green curve) functional interactions measured in participants ($n=6$) that had at least 2 responsive electrodes in both the temporal and frontal lobe during the observation of MIRC stimuli. The curves represent the average gPDC obtained from $n=3639$ pairs of frontal and temporal electrodes respectively. The two panels show the directionality of the functional interactions obtained when the gPDC was integrated in the lower ([13-30]Hz; panel **A**) or higher ([30-100]Hz; panel **B**) temporal frequency range respectively. Standard errors are shown but they are too small to be visible. Red-shaded areas mark intervals where the interactions in one direction are significantly stronger than in the opposite direction.