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The Ties That Bind: Agnosia, Neglect and Selective Attention to Visual Scale

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1 *Purpose of Review* Historical and contemporary treatments of visual agnosia and
2 neglect regard these disorders as largely unrelated. It is thought that damage to
3 different neural processes lead directly to one or the other condition, yet apperceptive
4 variants of agnosia and object-centered variants of neglect share remarkably similar
5 deficits in the quality of conscious experience. Here we argue for a closer association
6 between 'apperceptive' variants of visual agnosia and 'object-centered' variants of
7 visual neglect. We introduce a theoretical framework for understanding these conditions
8 based on 'scale attention', which refers to selecting boundary and surface information at
9 different levels of the structural hierarchy in the visual array.

10
11 *Recent Findings* We review work on visual agnosia, the cortical structures and cortico-
12 cortical pathways that underlie visual perception, visuospatial neglect and object-
13 centered neglect, and attention to scale. We highlight direct and indirect pathways
14 involved in these disorders and in attention to scale. The direct pathway involves the
15 posterior vertical segments of the superior longitudinal fasciculus that are positioned to
16 link the established dorsal and ventral attentional centers in the parietal cortex with
17 structures in the inferior occipitotemporal cortex associated with visual apperceptive
18 agnosia. The connections in the right hemisphere appear to be more important for
19 visual conscious experience, whereas those in the left-hemisphere appear to be more
20 strongly associated with the planning and execution of visually-guided grasps directed
21 at multi-part objects such as tools. In the latter case, semantic and functional
22 information must drive the selection of the appropriate hand posture and grasp points
23 on the object. This view is supported by studies of grasping in patients with agnosia and
24 in patients with neglect that show that the selection of grasp points when picking up a
25 tool involves both scale attention and semantic contributions from inferotemporal cortex.
26 The indirect pathways, which include the inferior fronto-occipital and horizontal
27 components of the superior longitudinal fasciculi, involve the frontal lobe, working
28 memory, and the 'multiple demands' network, which can shape the content of visual
29 awareness through the maintenance of goal- and task-based abstractions and their
30 influence on scale attention.

31
32 *Summary* Recent studies of human cortico-cortical pathways necessitate revisions to
33 long-standing theoretical views on visual perception, visually-guided action and their
34 integrations. We highlight findings from a broad sample of seemingly disparate areas of
35 research to support the proposal that attention to scale is necessary for typical
36 conscious visual experience and for goal-directed actions that depend on functional and
37 semantic information. Furthermore, we suggest that vertical pathways between the
38 parietal and occipito-temporal cortex, along with indirect pathways that involve the
39 premotor and prefrontal cortex, facilitate the operations of scale attention.

40
41 *Keywords:* *visual agnosia, object-centered neglect, selective attention, visual*
42 *perception, grasping, visual pathways*

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44

45 *Introduction*

46 *Visual agnosia* refers to any disorder in the visual recognition of objects that cannot be
47 attributed to more rudimentary visual defects in acuity, stereopsis, luminance or contrast
48 sensitivity, nor to higher-order cognitive functions such as verbal comprehension,
49 speech production, dementia, and more general memory or cognitive deterioration [1,2].
50 This definition means that visual agnosia is a multifaceted disorder, one that covers a
51 diverse spectrum of functions that are all required in order to accomplish the everyday
52 tasks of visual perception and recognition. Research on visual agnosia can therefore
53 serve two important functions. One is to better understand the nature of any specific
54 individual patient's disorder. The other is to inform our understanding of the functional
55 and anatomical organization of the human visual system. Both of these endeavors are
56 being rapidly enhanced by recent advances in neuroimaging and intra-operative
57 electrical mapping. Many excellent reviews and monographs on the topic of visual
58 agnosia already exist and we encourage the reader to consult them for either broad
59 overviews or for detailed expositions on specific topics [3-9]. Given this rich and
60 contemporaneous background literature, our aim here is to highlight certain facets of the
61 perceptual, as opposed to the semantic, symptoms of visual agnosia that we believe are
62 still poorly understood and that therefore could benefit from further critical consideration,
63 theorizing, and investigation.

64

65 We begin by revisiting Lissauer's [10,11] pioneering associative-apperceptive
66 dichotomy, a foundational pillar of visual agnosia, in order to underscore elements of his
67 conceptual framework that are understated in current textbook treatments. We then
68 review work involving two of the most extensively studied patients with visual agnosia,
69 "DF", and "HJA", who demonstrate unique patterns of perceptual and recognition
70 deficits in shape and scene processing. We survey evidence from these patients and
71 from patients with object-centered neglect that suggests that deficits in selective
72 attention to the parts of objects, and to the relations between object parts, can limit the
73 ability to bind various surface features and object parts onto a single object. This

74 problem with binding can also occur at a higher level in the structural description, such
75 as to the relations between objects, and even to the relations between different regions
76 in a scene. We refer to these functions collectively as the spatial scale of processing
77 and we limit their content to the structural hierarchy of the visual array. We further
78 acknowledge that selective attention to a specific spatial scale is necessarily
79 constrained by 'higher-level' sources of control over internal attention such as goal
80 selection. We move on to review the cortical network hubs associated with the control of
81 visual-spatial attention (often called 'orienting') and discuss a subset of visual neglect
82 characterized by object-centered deficits in perception. We offer candidate cortico-
83 cortical pathways that are capable of carrying the signals of selective attention to scale
84 to their cortical targets along the ventral occipitotemporal areas associated with visual
85 perception and visual agnosia. This analysis highlights the parallel nature of the neural
86 pathways out of visual cortex and their different cognitive and behavioural functions. It
87 also explains why damage that excludes the posterior parietal cortex can paradoxically
88 spare visually-guided grasping when directed towards simple goal objects and yet
89 impair grasping based on the most appropriate and contextually-meaningful part of
90 more complex objects, such as tools.

91

92 *Lissauer's patient "L"*

93 Lissauer's late 19th century studies of patient "L" constitute the earliest evidence that the
94 human visual system can be functionally (and anatomically) fractionated between brain
95 regions that support conscious visual experience and those brain regions that are
96 necessary for semantic elaboration [10,11]. L experienced great difficulty recognizing
97 objects, people, and places by sight alone despite intact central visual fields, preserved
98 fixation, smooth pursuit and saccadic eye movements, and relatively good acuity and
99 depth perception. Lissauer also reported that L could identify and describe common
100 objects when permitted to explore them haptically, when permitted to hear the canonical
101 sounds they could make, or when given their name verbally. Thus, both L's low-level
102 vision and his semantic knowledge of common objects remained intact, despite his
103 recognition deficit. These observations led Lissauer to conclude "...there must have
104 been a disruption of the associate processes." (p. 186), from damage to the pathways

105 linking the structures dedicated to apperception and those in which are stored the
106 associated semantic knowledge.

107

108 *Lissauer's notion of visual apperception*

109 Lissauer posited that the visual system's construction of "mental pictures", a process he
110 referred to as *apperception*, was functionally and anatomically distinct from the
111 *association* of those pictures with stored semantic information ("ideas"). Lissauer
112 described apperception as "...the stage of conscious awareness of a sensory
113 impression" (p. 181); "...the highest level of perception in which the conscious mind
114 takes a sensory impression with maximal intensity." (p. 182); "...the ability to detect
115 discrepancies between sense perceptions." (p. 183); and "...that function which enables
116 us to give information about the differences between sensory impressions." (p. 184). In
117 other words, Lissauer conceived apperception as the process by which we achieve a
118 visual percept, that is, a visual understanding of an object, which includes its shape or
119 structure, surface properties, and volume, and this process necessarily entails
120 discrimination.

121

122 Lissauer was determined to quantify visual percepts, but he realized that asking patients
123 to verbalize their conscious visual experience presumed the pathways linking 'mental
124 pictures' to their associated 'ideas' was intact. For example, Lissauer reported that
125 although his patient could not name colours by sight, he could successfully match and
126 sort colours when given samples, stating "If he was presented with samples of
127 Holmgren wools and asked to select all examples of the same shade he was able to do
128 this without hesitation. For example, he would select all the green shades and without
129 hesitation reject all blue colours or hues tending towards yellow. If he was presented
130 with a certain hue and asked to find its exact match, he was able to do this immediately.
131 He would either find the closest match or report that an exact match was not available.
132 Thus, he clearly was able to differentiate between subtle hues of grey, green, and
133 yellow." (p. 163). From this, Lissauer reasoned that quantifying visual percepts was best
134 approached using two possible non-verbal approaches. The first would involve
135 "...getting the subject to copy the stimulus either by drawing it or by repetition or

136 something along these lines.” (p. 183); The quality of the drawings and manner in which
137 they were made could provide insights into the quality of the patient’s visual
138 apperception. This approach is still used in more modern studies. In a second
139 suggestion, visual percepts could be quantified by measuring “The amount of difference
140 necessary for two percepts to be registered as being incongruent...” (p. 183). In other
141 words, the second method entailed the ‘bread and butter’ of visual psychophysics:
142 forced-choice measurement.

143

144 *Lissauer fractionates apperception and grounds it in spatial vision*

145 Lissauer further fractionated apperceptive visual agnosia into different domains. L’s
146 spared non-verbal colour discrimination, and his relatively intact ability to draw copies of
147 simple objects but his complete failure to copy more complex objects led Lissauer to
148 fractionate visual percepts into three domains “...the abilities to perceive colour, form,
149 and three-dimensional objects.” (p. 183). Lissauer’s distinction between simple and
150 complex objects anticipates a modern distinction between patients with form and
151 integrative visual agnosia, respectively, while Lissauer’s distinction between object
152 ‘form’ (2D) and 3D (real) objects anticipates Marr’s distinctions between the primal
153 sketch, 2 ½ D and 3D object model processing levels [12]. Furthermore, Lissauer’s
154 notion of visual apperception was fundamentally grounded in spatial vision. In fact, he
155 defended his entire notion of visual apperception by “...introducing spatial vision into the
156 framework...as a prerequisite for any complex visual perception, even if it is justifiable
157 to consider it an issue separate from apperception.” (p. 184). In other words, Lissauer
158 believed that spatial vision was a multimodal enterprise, referring to both retinal and
159 extra-retinal input, and suspected it was sufficiently complex to warrant its own system.
160 Damage to this system, he speculated, would result in a “chaotic” and “confusing” visual
161 experience that would disrupt object recognition. These speculations anticipate our
162 contemporary theoretical understanding of patients with simultanagnosia.

163

164 It is also worthwhile to point out that, contrary to many textbook characterizations of
165 Lissauer’s apperception-associative dichotomy, he did not believe the boundary
166 between these categories was strict. In fact, Lissauer stated "There can be no doubt

167 that our patient showed an impairment of apperception. In particular, as has been
168 described in the case history under the heading "form perception", his perception of
169 complex visual stimuli was not intact" (p. 185). Lissauer's conclusion flowed from his
170 observations of L's drawn copies of objects of various complexity. Recall that L
171 produced good line drawn copies of *simple* geometric shapes, but he became
172 hopelessly frustrated when attempting to copy more complex objects, and, regardless of
173 the object's structural complexity, L's drawings were made slowly, with concerted effort,
174 and in a piecemeal manner.

175

176 *Evaluating visual agnosia*

177 Patients who report impaired visual recognition are typically given tests for low-level
178 visual defects in acuity, contrast sensitivity, perimetry mapping, stereopsis, and depth
179 discrimination. Tests of object recognition entail asking patients to name and describe
180 objects in plain view and discriminate among them verbally or through gesture. The
181 additional information about 3D geometry and surface properties that are available with
182 real objects and models of real objects, relative to photographs or line drawings, can
183 improve recognition performance. In patients with visual agnosia, recognition improves
184 substantially when the experimenter uses non-visual means to cue object identity, such
185 as when they name the unrecognizable object; manipulate it in a way that produces its
186 canonical sound (e.g., shaking a set of keys to make a familiar sound of jingling keys);
187 or permit the patient to explore it haptically. Thus, patients with visual agnosia can
188 demonstrate that they possess accurate semantic information about the object that is
189 retrievable through non-visual sensory information. Aside from drawing copies of
190 objects from a visible template or one from memory, tests to reveal deficits in the
191 apperception of object structure or surface properties often rely on detection and
192 discrimination methods that are not dependent on verbal reports. For example, Efron
193 devised a two-alternative forced-choice (2AFC) test of object form discrimination in
194 which the participant indicates whether pairs of rectilinear shapes (squares and
195 rectangles) are the same or different [13]. The shapes themselves possess the same
196 texture, colour, and surface area, and differ only in terms of their lengths and widths.

197

198 Other tasks aim to test the integrity of representations of higher-order 3D structure.
199 Goodale and colleagues devised a version of Efron's shape-discrimination task using
200 3D blocks [14]. Taylor and Warrington devised an object-naming task in which
201 photographs of common objects were taken from conventional and unconventional
202 angles to test the patient's ability to access 3D information about the stimulus [15; see
203 also 16]. Variants of these tasks entail matching photographs of objects (or faces or
204 houses) taken from different viewpoints to a target photograph [e.g., 17]. Riddoch and
205 Humphreys devised displays in which line drawings of different objects are
206 superimposed on one another and the patient's task is to match the embedded objects
207 to samples presented in isolation [18]. Patients with deficits in figure-ground and part
208 segmentation perform poorly on this task [e.g.18-20]. De Renzi and colleagues devised
209 a match-to-sample task that pits visual structural similarity against semantic identity
210 [21]. In this task, three photographs are presented: the sample, the match, and the foil
211 Crucially, the match is the same object as the sample but is configured differently (e.g.,
212 an open vs. closed umbrella), while the foil is a different object but is configured in a
213 way that resembles the sample (e.g. a walking cane that resembles the sample closed
214 umbrella serves as a foil, when the match is the open umbrella) [22]. Patients with
215 visual associative deficits but relatively intact visual perception often choose the
216 structurally similar foil [22].

217

218 *Visual form agnosia*

219 The first patient demonstrated to possess visual form agnosia was "Mr. S", who was
220 systematically tested by Efron [13] and Benson and Greenberg [23]. Mr. S was unable
221 to name any common object or discriminate triangles from circles, despite being able to
222 identify colours, discriminate hue, and detect subtle differences in motion, luminance,
223 and overall size. Despite his deficit in shape perception, as far as a casual observer
224 could tell, Mr. S could reach for and grasp real objects accurately provided they were
225 moved by the experimenter, and he could localize small white pieces of paper on a
226 black background by pointing at them. Furthermore, he could name objects placed in
227 his hand and demonstrate their use through verbal or communicative gesture. Thus, his
228 semantic knowledge of objects was intact.

229
230 Mr. S's selective deficit was powerfully illustrated by his impaired performance when
231 copying from a visible template (see Fig. 1) and by his poor performance on Efron's
232 shape-discrimination task. In the shape discrimination task, the one that bears Efron's
233 name, a standard square and a rectangle are presented and the viewer is asked to
234 make a same-different judgment about the shapes of the two stimuli. The dimensions of
235 the rectangle are varied from trial to trial with the condition that it must always match the
236 square in terms of its surface reflectance and overall size. Mr. S's perceptual
237 impairments were also evident from the results of the attempts to train him to recognize
238 objects using his spared perceptual capacities. For example, he learned to correctly
239 name a red-backed playing card as a "playing card", but when he was presented with a
240 *blue*-backed copy of the same playing card, he could not name it at all. In fact, when Mr.
241 S was later presented with a red postage stamp, he identified it as the playing card. In
242 other words, Mr. S had relied on the colour of the object to cue its verbal identity.
243 Furthermore, if any of the objects he was trained to identify were placed on a different
244 background, he could no longer identify them properly. This was consistent with his
245 poor ability to trace the outlines of photographed objects. When doing this, Mr. S would
246 often leave the boundary of one object to trace the boundary of another where two
247 objects overlapped, suggesting impaired figure-ground separation. As compelling as the
248 evidence is for form perception in Mr. S's case, we do not know the exact location and
249 extent of damage to visual cortex he sustained, because detailed neural scans were not
250 available in the era in which he was reported.

251
252 The most extensively studied patient with visual form agnosia is "DF", and it just so
253 happens that her perceptual deficits are strikingly similar to Mr. S's. DF's visual fields
254 are intact well beyond central vision, her contrast sensitivity thresholds are normal at
255 high frequencies and modestly higher at lower frequencies, and her colour
256 discrimination remains largely preserved [24,25]. Nevertheless, she exhibits
257 prosopagnosia and possesses a profound deficit in object perception and recognition;
258 her drawn copies of line drawings are poor (see Fig. 1) and her performance on the
259 Efron shape-discrimination task is significantly impaired [24-26]; her match-to-sample

260 performance when line drawn objects are filled-in with black was at chance, regardless
261 of whether the objects are animals or simple geometric shapes [25]. Although her
262 recognition performance never approached levels observed in normally-sighted
263 populations, it improved when the test involved coloured photographs and real objects.
264 This is presumably because the additional spatial, colour, and surface cues to texture
265 and material properties facilitate the retrieval of intact semantic and structural
266 knowledge [26].

Mr. S. copies from...
memory

“circle” 

“square” 

“man” 

...a template



D.F. copies from...
memory

“apple” 

“sail boat” 

“ladle” 

...a template



H.J.A. copies from...
memory...

“lemon” 

“bee” 

“saw” 

...a template



Figure 1. Patient-drawn copies of objects. The structural components of the objects can come from (1) long term memory, as happens when the experimenter names an object aloud and the patient must recall and visualize the structural features of the object, and maintain them in working memory, visualizing them while translating their visualization into appropriate pen or pencil strokes on paper (left column); or (2) a real object or a picture (right column), photograph, or 3D model of an object, which the patient is asked to draw a copy of, therefore circumventing, to some extent, visualization and explicit long-term memory. For patients with visual form agnosia, such as Mr. S and DF, their copies from memory are relatively easily identifiable and are given reliably higher quality ratings by normally-sighted controls. In contrast, the patients' drawn copies of visible templates are often uninterpretable and are assigned reliably lower quality ratings by normally-sighted judges. In contrast to the drawn copies of patients with visual form agnosia, patient HJA's copies appear substantially better; his variant of visual agnosia leans more heavily towards the associative side of the apperceptive-associative spectrum. Nevertheless, it is important to note that in all cases the drawings are made laboriously – in a piecemeal fashion – which suggests that even HJA possesses impairments in visual perception. Indeed, HJA possesses deficits in segmenting overlapping objects, for example, which is one of several indicators for the integrative variant of visual agnosia.

313

314 Detailed MRI scans of DF's brain were taken at a number of different years following
315 her initial injury. The initial MRI scan revealed bilateral lesions to the ventrolateral areas
316 of her occipital cortex and bilateral lesions to the cuneus of dorsomedial occipital cortex
317 that were more extensive on the left than on the right [25]. These lesions have

318 expanded over the decades, particularly in the left posterior parietal cortex (PPC), but
319 functional MRI (fMRI) scans of DF's brain suggest that her primary visual cortex
320 remains functionally intact [27-29]. Consistent with the pattern of DF's recognition
321 deficits, fMRI scans reveal no differential activity while she viewed intact line drawings
322 or their scrambled counterparts [28]. Scans of normally-sighted individuals were made
323 under identical presentations to establish the regions that are typically activated when
324 viewing intact objects, their scrambled counterparts, and, importantly, the object-
325 preferential regions that are activated significantly more for intact objects than for
326 scrambled ones. When the group map of controls' object-preferential activity was
327 superimposed over DF's brain, the foci of activation were in the lateral occipital cortex
328 (LOC), precisely where DF's lesions were [28]. Notably, LOC is known to play a
329 prominent role in processing the outline shape and contour of objects [30-32; for review,
330 see 33]. When DF viewed grey-scaled and coloured photographs of real objects, stimuli
331 that improve her recognition performance, activation was observed in the intact areas of
332 her visual cortex, including the fusiform gyrus, lingual gyrus, and, to a lesser degree, the
333 collateral sulcus extending into parahippocampal cortex. Furthermore, activation in
334 these areas was positively correlated with DF's success or failure to identify the objects.
335 Notably, these same areas responded negligibly when she viewed scrambled versions
336 of those photographs [28].

337
338 While DF can classify scenes as natural or artificial at above-chance levels when they
339 are presented in full colour or in grayscale, her error rate increases substantially if the
340 scenes are presented in black and white, a finding consistent with her profound deficit in
341 shape perception [29]. In normally-sighted individuals, scene perception is associated
342 with a network of cortical structures, including LOC, the parahippocampal place area
343 (PPA), the retrosplenial complex (RSC; also referred to as the medial place area, MPA),
344 and the occipital place area (OPA) (for review, see 34). fMRI scans of DF's brain
345 showed greater activation in her intact parahippocampal gyrus when she viewed scenes
346 compared to when she viewed faces, suggesting she retains some functionality in the
347 scene-processing network, consistent with her ability to classify scenes relatively well
348 when they are presented in full colour [29].

349
350 For both scene and object perception, DF fares better when colour cues are available. In
351 normally-sighted individuals, the fusiform and lingual gyri, which border the collateral
352 sulcus in ventral occipitotemporal cortex, activate more strongly to visual surface
353 properties, including colour, specular highlights, shading, pattern, and texture, than they
354 do to object shape [35,36]. Activation in LOC shows an opposite preference, suggesting
355 a lateral processing preference for object shape and a more medial and anterior
356 processing preference for surface and material properties [35-40]. In line with the nature
357 of her deficit in shape perception, DF's performance in a three-item 'oddball task' falls to
358 chance levels provided the object-relevant property is shape alone [36]; When the
359 object-relevant property is texture, she performs at well-above chance levels, albeit still
360 below normal. In line with this dissociation, fMRI scans of DF's brain while she
361 performed these tasks showed there were no areas with greater activation for the
362 shape-discrimination task than for the texture-based one, whereas the middle and
363 posterior lingual gyrus and posterior fusiform gyrus showed greater activation for the
364 texture-discrimination task than the shape-based one [36]. The spared aspects of DF's
365 scene perception can be contrasted with the topographic associative agnosia
366 experienced by HJA, who is the most heavily studied patient with integrative visual
367 agnosia, a higher order visual disorder we turn to next, whose lesions are located more
368 medially and more anteriorly in the inferior occipitotemporal cortex.

369

370 *Integrative visual agnosia*

371 The term integrative agnosia was coined by Riddoch and Humphreys following a series
372 of experiments they conducted with patient HJA [17,18]. While in hospital for
373 appendectomy, HJA suffered a stroke perioperatively which left a large bilateral lesion
374 to the anteroventral half of his occipital cortex, extending about midway into temporal
375 cortex ventromedially. The stroke resulted in an upper field anopia and rendered him
376 achromatopsic, atopographic, prosopagnosic, alexic, and visually agnosic for common
377 objects [17,18]. Like DF, HJA's acuity and contrast sensitivity were relatively good, and
378 he had no trouble identifying and describing objects by touch [18,41] or describing
379 objects named aloud by others [18]. Unlike DF, however, he performed well at Efron's

380 shape- and line-orientation discrimination task [13], his line-copy drawings of simple and
381 real objects were good, and he was well above chance on a non-verbal object matching
382 task using pictures of common objects [18,19,41]. Thus, the pattern of visual deficits
383 indicated impaired access to stored semantic knowledge through sight alone, which
384 suggested his disorder leaned more closely towards the associative end of the visual
385 agnosia spectrum. Indeed, MRI scans of HJA's brain show that his lesions are more
386 anterior and more medial than DF's, encroaching well into the temporal cortex and
387 include the fusiform and lingual gyri, and the inferotemporal gyrus [19,41,42].

388
389 Although HJA's deficit does not conform to the pattern typical of visual form agnosia,
390 additional testing suggested he experienced apperceptive deficits. For example,
391 although HJA's copies of line-drawn objects were better than those done by patients
392 with visual form agnosia (see Fig. 1), his drawings were done in a time-consuming,
393 piecemeal fashion [18,41]. Furthermore, HJA's good object-matching performance
394 dropped substantially when the objects overlapped one another [18,19]. He was also
395 poor at classifying line drawings of objects as meaningful or meaningless, where the
396 meaningless objects were Frankenstein-like constructions comprised of component
397 parts from different objects [18]. HJA's identification performance for objects presented
398 in isolation was significantly worse when they were line drawings than when they were
399 silhouettes; The silhouettes lacked details within the object that might normally aid
400 recognition, but these details appeared to confound him. HJA also takes ~2-4 times
401 longer than controls do to determine whether two beads are located on the same or
402 different strings that overlap one another; and, when the strings are configured to
403 resemble amoebas, to determine if two beads are on the same 'string-amoeba' or
404 different ones, or if a bead is inside or outside of a single string-amoeba [19].

405
406 These observations suggested to Riddoch and Humphreys that HJA possessed a deficit
407 in the ability to construct not a coherent percept *per se* but one that reflected the object
408 in its entirety and in segmenting clusters of objects or scenes more generally. Although
409 HJA could rely on local geometric features to work out what an object was, he exhibited
410 signs of impaired perception of the relations between object parts and the object as a

411 whole. This idea is further supported by HJA's performance on a choice-discrimination
412 task that used Navon-like stimuli in which a large object, which constitutes the 'global'
413 level, is comprised of smaller objects, which occupy the 'local' level. In a popular task,
414 participants classify the global-level object as one type or another, while on other trials,
415 they classify the local-level objects as one type or another. When the global and local
416 levels share the same identity, they cue the same response and therefore operate
417 cooperatively. When the local and global levels differ, they can compete for different
418 responses provided the irrelevant level has been associated with a competing
419 response. However, when the irrelevant level is not associated with any response,
420 neither a cooperative nor a competitive effect is expected and the condition is
421 considered neutral. In normally-sighted individuals, performance is typically better when
422 the global and local level share the same identity and will show a modest discriminative
423 advantage for the global level over the local one. Using the letter-stimuli, however, HJA
424 is substantially slower and less accurate than controls. Moreover, although he shows an
425 advantage for the global level over the local one, his performance is slowest and least
426 accurate when classifying the local letters embedded in a neutral global one, suggesting
427 a particularly strong interference effect transitioning from the global to the local scale,
428 regardless of competing stimulus-identity and response associations [19].

429

430 *Attention, spatial vision, and visual agnosia*

431 HJA's deficit in integrating object components into a coherent whole and segmenting
432 overlapping objects reflects a deficit in the ability to integrate levels of the visual
433 structural hierarchy. By "structural hierarchy" we are referring to the way in which every
434 visual scene can be thought of as comprised of local and global geometric elements
435 relative to one another. Just as a laptop on a desk forms part of a larger scale desktop
436 scene or an even larger office scene, the visual structure of a laptop is comprised of
437 various smaller-scale components (e.g., screen, keyboard, touchpad), each of which
438 can be further segmented. A keyboard, for example, can be subdivided into keys, each
439 of which assumes one of a few different shapes and are positioned at different locations
440 within the keyboard. Each key possesses a printed letter or symbol, most of which can
441 be further subdivided into component contours and lines. Farah [6,43] suggested that

442 selective attention played a crucial role in mediating the relationships between objects
443 and among the parts of objects. In other words, Farah believed selective attention
444 played a crucial role in shifting ‘the mind’s eye’ within and between levels of the
445 structural hierarchy.

446

447 Using this theoretical perspective, Farah [6] argued that damage to selective attention of
448 this nature could manifest, albeit rarely, in patients with what she referred to as “dorsal
449 simultanagnosia”. The dorsal reference stemmed from the preponderance of cases with
450 damage to dorsal parietal occipital cortex (POC) who exhibited this behaviour. Farah
451 wrote that the reported propensity of some of these patients to fixate on the parts of
452 objects rather than the whole reflected a deficit “... with *seeing* objects, or seeing them
453 at the “correct” level of the hierarchy of part-whole analysis; whatever dorsal
454 simultanagnosics can see, they can recognize.” (p. 38, [6]). The emphasis Farah placed
455 on the word ‘seeing’ suggests that she was referring to the content of visual awareness
456 in these patients – their visual phenomenology. At the same time, Farah noted that,
457 somewhat paradoxically, a deficit in the ability to transition between levels of structural
458 hierarchy can arise from damage to ventral cortical structures. Farah referred to these
459 cases as instances of ventral simultanagnosia. She used the term ‘ventral’ because the
460 location of damage tends to occur in ventral occipito-temporal cortex; and she used the
461 term ‘simultanagnosia’, because these patients have demonstrated impairments with
462 discriminating and reporting the letters of relatively simple and briefly presented three-
463 letter words and non-words [6,44].

464

465 Notably, the similarity of symptoms between dorsal and ventral simultanagnosia leaves
466 open the possibility that deficits in transitioning between and within levels of the
467 structural hierarchy of the array might arise from damage to the pathways that carry
468 signals between posterior parietal and occipito-temporal cortex. It is notable that HJA,
469 whose damage is restricted to ventromedial occipital-temporal cortex, exhibits his
470 strongest impairments when recognizing scenes, which occupy the pinnacle level of the
471 visual structural hierarchy and entails small and large-scale processing; when isolating
472 overlapping objects, which requires assigning the parts of multiple objects to their

473 appropriate wholes and entails competition within scales and similar levels of the
474 structural hierarchy; and when matching objects when their parts are substituted for the
475 parts of other objects. This pattern of deficits is consistent with what might be expected
476 to occur following damage to structures that integrate information within and across
477 different levels of the structural hierarchy [45]. Put another way, HJA's behavior implies
478 that damage to brain circuits that assemble visual representations at different scales of
479 integration can contribute to visual agnosia. In a subsequent section, we discuss further
480 evidence that is consistent with this viewpoint, based on neuroimaging work in normally-
481 sighted individuals and in patients with visual agnosia and spatial neglect. Nevertheless,
482 it is first important to clarify what is implied by the term selective attention as it relates to
483 structural hierarchy.

484

485 *Selective attention and attention to scale*

486 The term selective attention is used in the cognitive sciences to refer to a wide variety of
487 perceptual functions, including the selection of various spatial locations for privileged
488 processing [46], the selection of particular surface and material properties such as
489 luminance, color, and texture [47], the selection of objects and extended surfaces [48],
490 and even the selection of some items over others that have been stored in working
491 memory [49; for review see 50]. The form of selective attention implied by Farah [6] is
492 distinct from all these, since it refers to one or more of the many levels of structural
493 description for a scene or object. Other researchers have referred to this form of visual
494 selection as attention to the local versus the global aspects of a display [51,52] and as
495 attention to scene scale [53]. Each of these terms necessarily implies selective attention
496 to some aspects of space, to some features, to some objects, to some surfaces and so
497 on, but attention to each of these visual properties is circumscribed by the level in the
498 hierarchical description of a scene that is required to accomplish a perceptual task (e.g.,
499 "attend to the shape of the tree" versus "attend to the shape of the forest").

500

501 Selective attention to one level of scene scale over another level necessarily involves
502 aspects of visual function that have traditionally been studied under the separate
503 umbrellas of spatial attention (e.g., 46), attention to features [47,54,55], and object-

504 based attention (e.g., 48,56,57). Yet note that the task of selectively attending to one
505 scene level over another means, by definition, that attention to spatial locations, featural
506 properties, and objects are not independent. Selecting any level of the scene hierarchy
507 implies attention to locations, features, and objects at that scale. For example, when
508 selecting at the level of “graspable object”, the object must be segmented from the
509 surface it rests on and the background behind it (separating figure from ground), and
510 the object’s location within the visual array, its spatial relationship between it and parts
511 of the viewer’s body (e.g. eyes, head, and limbs), its surface properties such as its
512 texture and its volumetric shape at different scales (e.g., curved vs. rectangular at larger
513 vs. smaller scales) must all be registered by the motor system to successfully guide the
514 hand to grasp and manipulate the object appropriately.

515

516 From this perspective, it is informative to discuss the effects on DF, who possesses
517 visual form agnosia, of manipulating selective attention at the level of objects. Normally-
518 sighted and neurologically-intact individuals are generally slower to discriminate targets
519 that are preceded by invalid spatial cues (for a review see 58). This cost is associated
520 with the processing time it takes for spatial attention to disengage the cued location and
521 engage a different location that the target occupies [46,59]. The crucial twist to this
522 finding is that participants are faster to respond if the target and a preceding spatial cue
523 are located within the boundaries of the same object, even when the spatial cue is
524 invalid [48]. In other words, the boundaries of the object define a local region in which
525 selective attention can spread, reducing the processing costs of reorienting attention to
526 a new location that would ordinarily occur on invalidly cued trials. This effect is thought
527 to operate in conjunction and in parallel with spatial attention and has been called
528 ‘object-based attention’ [48,56,57]. When DF performs a standard spatial-attention task,
529 her processing time costs for invalidly-cued spatial targets are akin to those observed in
530 normally-sighted controls. Furthermore, like in normally-sighted controls, she showed
531 greater processing costs for vertical over horizontal shifts in cued spatial attention [60].
532 Thus, DF’s spatial attention appears to be intact. Importantly, however, DF did not show
533 the typical advantage for within-object spatial cueing over between-object cueing [60]. In
534 fact, her performance, unlike that of the controls, merely reflected a known increased

535 processing cost for vertical shifts in attention over horizontal ones, whereas, for the
536 controls, this cost was overcome provided object-centered attention was invoked [60].
537 Thus, for DF, damage to LOC meant that there was no shape content or shape
538 processing for object-centered attention to operate on.

539

540 These results of object-centered attention measures in DF suggest that structures in
541 visual cortex that are dedicated to processing object form, which are damaged in her
542 brain, are recipients of the modulatory influence of spatially-cued attention on
543 performance. The neural correlates of attention in an object-centered context have also
544 been studied using tasks in which participants attend to one or the other of two
545 superimposed images, not unlike the superimposed image recognition and
546 discrimination tasks on which many patients with visual apperceptive agnosia exhibit
547 performance deficits. Two advantages of using superimposed stimuli are that (1) they
548 control for differences in low-level visual features, because the visual input is identical
549 across two or more tasks, leaving the perceptual and cognitive operations performed on
550 the visual input to systematically differ; and (2) they control for large-scale spatial
551 attention. When participants view an image of a house and a face superimposed on one
552 another, for example, activation in PPA is enhanced whenever attention is deployed to
553 the house, while activation in the fusiform face area (FFA) is enhanced whenever
554 attention is deployed to the face [61-64]. Orienting attention from one image type to the
555 other is associated with the ventrolateral prefrontal cortex, the posterior superior parietal
556 cortex, and ventral occipito-temporal cortex. Furthermore, consistent with feedback
557 based on attentional modulation, enhanced activity in the PPA and FFA is associated
558 with local potential responses occurring ~200 ms or later, well after image onset [61].
559 These studies highlight the influence of attention on visual perception across different
560 stimulus classes in ventral visual cortex.

561

562 Support for the view that selective attention to scale aids the construction of the content
563 of visual awareness comes from studies that induce inattention blindness (for review,
564 see 65). In these studies, participants perform difficult tasks wherein they are asked to
565 track, detect, or classify stimuli under attentionally-demanding conditions and the

566 difficulty of the task is varied in order to induce inattention blindness. In some task
567 variants, participants track moving objects or count the number of instances in which
568 they see a number during a rapid serial visual presentation (RSVP) of images. The
569 primary target stimuli are mixed into a 'noise' background comprised of, for example,
570 random patches of different colours. On critical trials an unexpected scene or object is
571 presented, and participants are asked if they were aware of anything different on that
572 trial. When the primary task difficulty is increased, for example, by increasing the speed
573 at which the tracked-stimuli move, participants typically fail to notice unanticipated
574 scenes [66]. Inattention blindness and dual-task paradigms have also been used to
575 demonstrate the importance of attention for the extraction of summary statistical
576 information about variance in the colour and size of ensembles of objects [67].
577 Interestingly, the perception of scenes and ensembles and the neural correlates of
578 these processes has been both behaviourally and anatomically linked: performance on
579 scene-perception tasks is correlated with performance on ensemble-perception tasks
580 [68] and scenes and object ensembles are processed in overlapping structures
581 bordering the collateral sulcus in ventral visual cortex [69-72], areas that are damaged
582 in patient HJA.

583
584 *The cortical structures associated with the control of selective attention to scale*
585 Figure 2 highlights the visual pathways out of occipital cortex that serve visual
586 perception and the pathways out of the dorsal and ventral parietal attentional centres of
587 the superior and inferior parietal lobe, respectively, that putatively influence visual
588 perception. The upper panel shows a ventral view of the right hemisphere and
589 schematically illustrates, in orange, yellow, and red, the following well-established
590 pathways: the inferior longitudinal and inferior fronto-occipital fasciculi (IFL and IFOF)
591 and the occipito-temporal projection system (OTPS), that deliver visual signals out of
592 occipital cortex to the temporal and prefrontal cortex.

593
594 The lower panel of Figure 2 shows a three-quarter view of the posterior right
595 hemisphere and overlays schematic illustration of the pathways out of parietal areas
596 that are associated with the control of selective attention to scale and those associated

597 with higher-level cognitive operations. The more recently studied subset of these
598 pathways, illustrated in light green, interconnects the intraparietal and posterior inferior
599 parietal attentional centers in the intraparietal and posterior inferior parietal cortex to
600 structures in the occipito-temporal and temporal cortex that are associated with visual
601 perception. These pathways can potentially carry selective attention signals directly,
602 and therefore rapidly, between the attentional centres and the visual cortical structures
603 necessary for the typical construction of the content of visual awareness. These direct
604 pathways are well-positioned to aid not only in the construction of moment-to-moment
605 phenomenological vision, but also in the selection of semantic information stored in the
606 temporal lobe necessary for the selection of appropriate grasp points on complex
607 objects, such as tools, that are suitable for their intended use.

608

609 The pathways illustrated in blue in the lower panel of Figure 2 reflect connections out of
610 the dorsal attention hub of the superior parietal lobule that interconnects the superior
611 parietal and intraparietal cortices (SPC and IPC) and dorsal prefrontal and premotor
612 cortex, bilaterally, and includes core areas that are engaged when attention is
613 voluntarily deployed from one spatial location to another and during the planning and
614 execution of eye movements [73,74]. The ventral subnetwork is lateralized to the right
615 hemisphere and is comprised of structures in the ventral prefrontal cortex and the
616 ventrolateral inferior parietal cortex, caudal superior temporal cortex, and the anterior
617 dorsolateral occipital cortex [73,74]. Both subnetworks are associated with the
618 intentional deployment of spatial attention and its maintenance, but the ventral
619 subnetwork is engaged when covert attention is 'captured' by stimuli that possess
620 salient and task-relevant components [73,74].

647 *Visuospatial neglect and selective attention*

648 Neglect is conventionally considered a deficit in deploying spatial attention to objects in
649 the contralesional field [75]. As we have discussed, this function is closely associated
650 with the dorsal and ventral attention subnetworks [73,74]. Classic methods for testing
651 neglect include the line-bisection task [e.g., 76,77], in which the patient is asked to
652 indicate the center of a line that is oriented from left-to-right, and cancellation tasks [e.g.,
653 78,79], in which the patient is presented with a cluttered page illustrated with objects
654 and is asked to mark each one of the objects or instances of a particular object amongst
655 a mix of different object types. In both tasks, the patients perform as if they are biased
656 towards the ipsilesional side of the line or page. In other words, the patient behaves as
657 if they ignore the side of space that is opposite to the hemisphere their lesion is located
658 in [80]. Lesion analyses of patients with spatial neglect reveal right-hemispheric damage
659 to the ventral subnetwork, including the superior temporal gyrus, supramarginal gyrus,
660 angular gyrus, inferior and middle frontal gyri, the anterior insula, the frontal operculum,
661 and the white matter pathways that underly these areas [81-88].

662
663 Like visual agnosia, more recent research with neglect patients is based on a diverse
664 set of tasks. Contemporary assessments for spatial neglect contain combinations of
665 tests like line bisection, cancellation, figure copying, representational drawing (see, for
666 example, the Behavioral Inattention Test [89]), and word and sentence reading tasks
667 [e.g., 90]. Crucially, performance on assessments for neglect can vary considerably
668 from patient to patient. In fact, double dissociations have been demonstrated where one
669 patient exhibits neglect in one subtest (e.g., line bisection) but not another (e.g.,
670 cancellation), whereas another patient exhibits the reverse pattern [91]. Double-
671 dissociations such as these indicate that these tests recruit different underlying
672 processes and neural substrates that can be damaged independently. Thus,
673 visuospatial neglect, like visual agnosia, does not constitute a uniform disorder (for
674 reviews see [90,91]). Indeed, recent lesion analyses accommodate these differences by
675 categorizing tests based on whether they rely more heavily on patient-centered (i.e.
676 egocentric) spatial reference frames, which characterize the more classic symptoms of

677 neglect that are tethered to the patient's contralesional visual field or side of space, or
678 on object-centered reference frames, which we discuss in the next section.

679

680 *Object-centered neglect and object-centered attention*

681 Despite the conventional viewpoint that neglect is a deficit in deploying spatial attention
682 to the visual field or side of space opposite the hemispheric side of the lesion [75], it is
683 clear that a subset of neglect patients experience deficits in object-based perception,
684 regardless of the object's location in the visual field [92,93] (for review see [75,93]). One
685 set of tests that highlight the object-centered aspects of neglect are cancellation tasks
686 [94,96,97]. In these tasks, the patient is presented with a scene of items and is asked to
687 indicate target items. They are elegant because the patient views the same visual scene
688 and, therefore, the experimenter can manipulate the scene itself while keeping the task
689 demands the same or they can keep the scene the same while manipulating the task
690 demands [98]. In some versions of the task, the targets appear scattered throughout the
691 scene, embedded in a background full of distractor items. In a pioneering study by
692 Driver and Halligan, two groups of multiple short lines were distinguished by colour and
693 located on opposite sides of the display [94]. The patient's task was to cross each line
694 out, regardless of which group the line belonged to, under conditions of free viewing in
695 which neither the patient's eyes nor the head are fixed. Remarkably, the patient omitted
696 lines to the left *within both groups* [94]. It was as if the lines were grouped into a holistic
697 unit, presumably driven by the Gestalt principles of proximity, similarity of form and
698 colour, and by figure-ground separation. Thus, this finding suggests that visual neglect
699 can impair Gestalt-grouping processes that integrate spatial and object information –
700 the very processes that would aid ensemble perception.

701

702 The cancellation task was enhanced by Ota and colleagues, who created a scene
703 comprised of two target types that differed from one another by only a subtle change in
704 one of their parts [99]. Circles, for example, served as one target type while variants of
705 the circle that had a small gap in them on either the left or right side served as a
706 second, 'partner' target type. A variant set of target types was created that was
707 comprised of triangles and trapezoids. The latter were made by flattening one of the

708 corners of the triangle, such that the two object types were distinguishable merely by
709 this flattened part, which, like the gap, could occur on the left- or right-side of the
710 triangle. The task was to indicate each instance of one object type with one kind of mark
711 (e.g., circling the triangles) and to indicate each instance of the other, 'partner' object
712 type with a different mark (e.g., crossing-out the trapezoids) [99].

713
714 Ota and colleagues tested two patients. The first patient possessed lesions to the
715 insula, anterior superior temporal gyrus, and inferior frontal gyrus. In accordance with
716 classic egocentric or patient-centered neglect, this patient tended to miss targets
717 located to the left-hand side of the page, regardless of what target-type they were. The
718 second patient possessed lesions that were more posterior, involving the angular gyrus
719 and posterior superior and middle temporal gyri. Interestingly, regardless of where the
720 first target type (triangles or circles) was located on the page, this patient performed just
721 as well as the first had for targets located in their ipsilesional (i.e. 'good') field. In other
722 words, the second patient with more posterior damage showed no unusual tendency to
723 miss targets in contralesional space. Crucially, however, this patient omitted targets
724 when the distinguishing part of those targets occurred on the left-side of the object,
725 regardless of where the objects were located in the scene, indicating a deficit in
726 attention to local-scale in the contralesional side of the object.

727
728 *Lesion analyses reveal the neural correlates of object-centered neglect*

729 A number of groups have used lesion analytical techniques to identify abnormal voxels
730 in large groups of neglect patients relative to neurologically intact or neurologically
731 compromised controls. The analysis involves correlating these abnormal voxels with
732 different symptoms as assessed by different tests. Chechlacz and colleagues
733 administered a modified version of Ota's cancellation task, called the apples-
734 cancellation task to 41 patients in order to quantify the severity of patient-centered and
735 object-centered neglect [81]. In-line with the view that object-centered and patient-
736 centered neglect were distinct subcomponents, they found that the severity of deficit in
737 each was uncorrelated. Additionally, the voxel-based analytical techniques that involved
738 morphometry and lesion-symptom mapping provided converging support for separate

739 clusters of regions underlying patient- and object-centered neglect. Regions associated
740 uniquely with object-centered neglect were located in the posterior right hemisphere and
741 included the right middle occipital gyrus, the angular gyrus, and adjacent posterior
742 regions of the inferior, middle, and superior temporal gyri. These analyses also
743 identified the superior longitudinal fasciculus, the inferior fronto-occipital fasciculus, and
744 the inferior longitudinal fasciculus, suggesting the involvement of these pathways in
745 selective attention to scale.

746
747 Verdon and colleagues tested 80 patients with a battery of tests in order to perform a
748 principal components analysis on the resultant scores to discover latent factor
749 groupings of the tests. Among the tests was the Ota cancellation task and a similarly
750 constructed compound-word reading task, which entails separately tabulating the
751 number of omissions of the whole word as a function of the side of the page the word
752 appears in, along with tabulating the number of omissions of the left- and right-word of
753 the compound words, regardless of where they occur on the page. Verdon and
754 colleagues performed voxel-based lesion-symptom mapping (VBLM) which combined
755 the patient-specific factor scores, which were derived from the battery of 'pen and
756 paper' tests, with the MRI scans of the patients' brains [88]. They found three factors
757 that accounted for 82.1% of the test score variance. Again, in-line with the view that
758 object-centered neglect is a separate component of neglect, the object-centered
759 components of the Ota cancellation and word-reading tasks loaded strongly and
760 *uniquely* onto one of the three dominant factors [88]. Furthermore, the patient scores for
761 this factor correlated less with the other two factors than the patient scores for the other
762 two factors correlated with one another, reinforcing the notion that the object-centered
763 components of the test probe a distinct function [88]. The VBLM localized the structures
764 associated with this distinct function: Variance in the object-centered factor was
765 maximally associated with damage to the white matter adjacent to the middle temporal
766 gyrus [88], indicating a crucial role in the long white matter pathways connecting the
767 occipital cortex to the temporal and frontal cortices in scale attention. Of the patients
768 with the most severe deficits on the object-centered tests, half possessed lesions
769 extending from the occipital to the medial temporal lobe, whereas the other half

770 possessed lesions that extended more laterally and anteriorially into the temporal cortex
771 [88]. This final observation might reflect a difference in linguistic emphasis between the
772 two object-centered tasks, with poor performance on the non-linguistic Ota task
773 associated with damage to the posterior regions.

774
775 Chechlacz and colleagues used anatomic likelihood estimation to perform a meta-
776 analysis of 10 lesion-overlap studies that involved a combined 700 patients with
777 visuospatial neglect [82]. The analysis separated tasks that were geared to reveal
778 patient-centered impairments from those geared to reveal object-centered ones.
779 Regions associated with object-centered deficits were located entirely in the parietal
780 and occipital cortex. The clusters with the largest ALE values included the right posterior
781 middle temporal gyrus and adjacent white matter pathways of the posterior superior
782 longitudinal fasciculus (SLF), the right middle occipital gyrus, the anterior angular gyrus,
783 the IFOF, and the white matter underlying the anterior superior parietal lobule (SPL).
784 Again, these findings imply that object-centered neglect is associated with damage to
785 cortical regions associated with visual perception, the ventral attention network, and the
786 pathways that likely carry signals from these areas to prefrontal targets, suggesting
787 these structures are involved in constructing object-centered content of visual
788 awareness.

789
790 *Pathways involved in selective attention to scale*

791 The notion that selective attention to scale plays a role in the mental construction of
792 objects and scenes is supported by the connectivity of the vertical and posterior-most
793 components of the SLF, illustrated schematically by the light green lines in the lower
794 panel of Figure 2. These cortico-cortical components would be capable of carrying
795 attentional signals directly between the dorsal and ventral subnetworks along the
796 intraparietal cortex (IPC) and temporal-parietal junction (TPJ) and inferior
797 occipitotemporal cortex, where damage is associated with visual object agnosia. The
798 figure also makes clear the long horizontal connections to cortical targets in the
799 prefrontal cortex through which dorsal and ventral parietal attention subnetworks
800 operate indirectly on visual perception. These regions control eye movements (e.g.,

801 frontal eye fields) and host broadly distributed executive responsibilities that require
802 control over 'internal' attention for goal, task, and response selection and inhibition,
803 spatial and verbal working memory and visual search (e.g., [100-102]) and closely align
804 with the set of cortical structures that comprise a multiple demands network [103].
805 Duncan has argued that the role of this large network is to construct what he refers to
806 as 'attentional episodes' over brief task epochs during which the network configures and
807 structures cognition (and constituent processes) suitably for solving a sub-goal on its
808 way to completing the task [104,105].

809

810 *Ventral visual perceptual pathways out of occipital cortex*

811 There are at least five major intra-hemispheric pathways along which visual information
812 is conveyed between the occipital lobe and the rest of the brain: the inferior longitudinal
813 fasciculus (ILF), the medial longitudinal fasciculus (MLF), the superior longitudinal
814 fasciculus (SLF), the inferior fronto-occipital fasciculus (IFOF), and the occipito-temporal
815 projection system (OTPS). The ventral visual pathways that are well-studied and closely
816 associated with visual perception (the OTPS, ILF, and the IFOF) are schematically
817 illustrated in orange, yellow, and red, respectively in Fig. 2. These three pathways
818 complement one another. The long, horizontal connectivity of the ILF [106-109] and
819 IFOF [110-113] afford direct and rapid transmission of visual information between lower
820 and higher levels of the visual processing hierarchy and prefrontal structures associated
821 with executive processing, respectively. These pathways are thought to support the
822 rapid construction of initial estimates, 'hypotheses', or 'primitives' of higher-level
823 descriptions of the content of the visual array (e.g. [114]). These primitives can then be
824 reinforced or rejected with subsequent volleys of visual input through the serial,
825 stagewise U-shaped and neighborhood-fibre projections of the OTPS, which help refine
826 lower- and intermediate-level structural descriptions [106,115]. Thus, the ILF, OTPS,
827 and IFOF are crucial bidirectional pathways that transmit visual sensory input for
828 elaboration and integration with semantic information in the medial temporal lobe. The
829 SLF, on the other hand, can be subdivided into pathways responsible for the regulation
830 of spatial attention, which are shown in Fig. 2, for conveying visual input to the

831 sensorimotor structures of the posterior parietal and premotor cortices, and for the
832 production and comprehension of speech.

833

834 *Electrical stimulation of the ILF and the IFOF*

835 The involvement of the ILF and IFOF in visual object processing is further supported by
836 electrical brain mapping studies of patients undergoing awake surgical resection for
837 small lesions in posterior temporal or occipitotemporal cortical areas adjacent to the ILF
838 and in the superior temporal, inferior parietal, and frontal cortical areas adjacent to the
839 IFOF. Mandonnet and colleagues found that stimulation at the junction between the
840 fusiform and inferior temporal gyrus elicited errors when the patient named common
841 objects presented as line drawings [116]. Their patient misidentified, for example, an
842 armchair as a mirror and a mask as a cat. What is interesting about the nature of these
843 errors is the structural similarity between the object depicted and the one perceived (see
844 Fig. 3). The back of the armchair resembles a classic, hand held ovoid mirror, complete
845 with a curvilinear line inside it that is intended to illustrate the convexity of the chair's
846 back-cushion but could be mistaken for glare or the reflection of a curvilinear object in
847 the hand-held mirror. Interestingly, a failure to integrate the legs of the chair into the
848 percept would exacerbate the misperception of a mirror, as would a reliance on part-
849 based recognition.

850

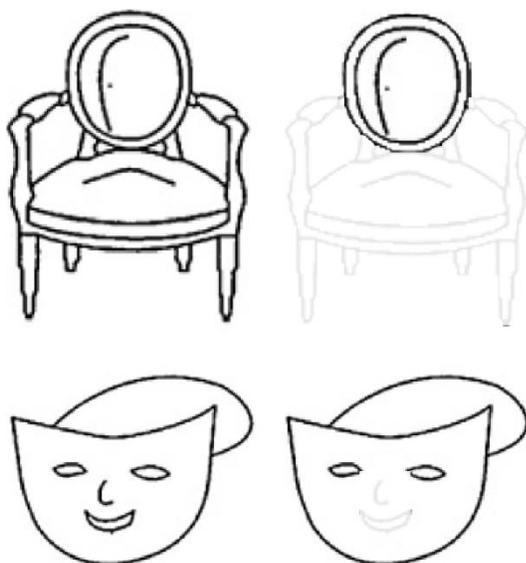


Figure 3. Two sample images from the Boston Naming task that were misnamed (left), along with their putative 'percepts' when patients were undergoing electrical stimulation (right) [116]. Top left: chair; Bottom left: mask. The pictures on the right represent possible 'mental pictures' (percepts) that result from failures of selective attention to scale rather than mere failures to name what is seen. The top right panel illustrates what might result from a failure to select and integrate the seat, legs and arms of the chair, leaving only the back of the chair, which does resemble a mirror complete with a minor reflection. The bottom right panel illustrates what might result following a failure to select and integrate the nose and mouth of the mask, resulting in something that resembles a cat. The mask's string is misinterpreted as the body of a resting cat.

869
870 Recall that HJA's reliance on part-based recognition led him to misidentify line drawn
871 objects and that his recognition performance improved when the local details of line
872 drawn objects were removed by filling the object in with black to create silhouettes. For
873 the case in which the electrically-stimulated patient misidentified the mask as a cat, a
874 failure to consider the detail of the mouth cut-out of the mask, and an over-reliance on
875 the top of the mask, which resembles the ears of a cat, helps explain the
876 misidentification error. Furthermore, the mask's string can be misinterpreted as outlining
877 the boundary of a cat's body. A failure in figure-ground segmentation for the space
878 between the string and the mask as background, therefore, can also help explain the
879 error. Remarkably, this patient also reported that the line drawings appeared 3D during
880 stimulation, highlighting the importance of visual depth processing and spatial vision as
881 Lissauer argued over a century ago. Notable too, is that the spherical resection (~1.5
882 cm) was localized to the right ventrolateral occipital cortex and resulted in novel
883 postoperative central visual deficits in shape, face, and word perception [116]. Although
884 these deficits were resolved three months after surgery [116], these observations
885 suggests that these regions were crucially involved in object-based visual perception
886 before, presumably, neural plasticity allowed other regions to assume the role of the
887 lesioned structures.

888
889 Coello and colleagues used a similar task, this time presenting two pictures, one to
890 each visual field [117]. Subcortical stimulation of the ILF above the right fusiform gyrus
891 resulted in failures to name the picture presented in the left visual field but no failure to
892 name the picture presented in the right visual field. The patient affirmed they saw the
893 object, denying any visual disturbance, yet could not name it, suggestive of pure optic
894 aphasia. In two additional patients, intraoperative stimulation of the ILF led to
895 impairments in reading short sentences and in symbol recognition [118]. These patients
896 remarked that they experienced difficulty combining individual letters into intelligible
897 words and were only able to spell words letter-by-letter, which is strikingly reminiscent of
898 Farah's descriptions of 'ventral simultanagnosia'.

899

900 Electrical stimulation to the surface of the posterior aspect of the left middle and
901 superior temporal gyri and to the IFOF beneath the superior temporal sulcus also
902 induces picture-naming errors on the Pyramids and Palmtrees Task [120-122]. In this
903 task, three line-drawings are shown to the participant, a sample, its semantic match,
904 and a distractor. For example, a pair of hands should be matched with its target, a pair
905 of gloves, as opposed to the distractor pair of shoes. The participant's task is to point to
906 the semantic match (the pair of gloves, in the example given). Electrical stimulation to
907 the IFOF produced incorrect or no responses whatsoever, with some of the patients
908 expressing confusion about what they were looking at [120,121]. Taken together, the
909 evidence suggests that these ventral pathways are crucial for transmitting attentional
910 and structural information to posterior ventral areas involved in the mental construction
911 of conscious visual experience and the downstream anterior areas involved in linking
912 percepts with their associated semantic features, including their verbal labels.

913

914 *Electrical stimulation of ventral occipito-temporal cortex and high-level visual perception*

915 Recent studies have demonstrated that high-level cortical regions within the ventral-
916 stream of visual processing are associated with the mental construction of conscious
917 visual experience. For example, Parvizi and colleagues studied a patient who had
918 electrodes implanted into his right inferior temporal lobe, to probe the location of
919 pharmaceutically-resistant seizures [123]. Electrical stimulation of two of these
920 electrodes, which were located on the posterior and middle aspects of the lateral bank
921 of the right fusiform gyrus (i.e., overlapping FFA, as confirmed in a separate fMRI
922 session), had a striking effect on the patient's conscious perception of faces. Namely,
923 the stimulation caused the patient to experience facial hallucinations, during which he
924 remarked "You just turned into somebody else. Your face metamorphosed", and "You
925 almost look like somebody I've seen before, but somebody different. That was a trip....
926 It's almost like the shape of your face, your features drooped" (both p. 14918) [123].
927 Importantly, electrical stimulation of these electrodes did not produce the same effect
928 when viewing non-face objects, and sham stimulation of these electrodes and
929 stimulation of nearby, but non-face-selective electrodes did not cause distortions in the
930 patient's perception of facial features [123].

931
932 Mégevand and colleagues examined a patient who was undergoing presurgical
933 evaluation for treatment-resistant epilepsy and had several electrodes implanted into his
934 right frontal and temporal cortices [124]. Separate fMRI and intracranial
935 electroencephalography (iEEG) sessions determined the location and functional
936 responsivity of scene-selective regions of cortex in the medial fusiform gyrus and
937 collateral sulcus, overlapping the parahippocampal place area (PPA) [124]. Direct
938 electrical stimulation of these regions induced topographic, scene-based hallucinations
939 based in part on the patient's memories of particular places. For example, the patient
940 reported seeing his optometrist's office and on a separate occasion a train station in his
941 neighbourhood [124]. Taken together, these findings from the electrical stimulation
942 studies of FFA and PPA results strongly suggest a causal role for these structures in the
943 construction of our moment-to-moment visual experiences of face and scene-based
944 perception.

945
946 *Parallel visual object and spatial processing*
947 Studies of visual agnosia have also helped illustrate the parallel nature of visual
948 processing across different functional and behavioural end-points. These issues have
949 been studied in the context of reaching out to grasp and manipulate objects in a few
950 visual agnosics, most notably DF and HJA. To reach out and grasp an object
951 successfully, the visual system must analyze the 3D geometry of an object and combine
952 this analysis with the agent's goal and stored functional information about the object in
953 order to select grasp points along with an appropriate grasp type (e.g., a whole hand or
954 a pincer grasp). This suite of information must also incorporate a set of unintuitive
955 spatial relationships among our limbs, body, head and eyes, and the object itself. All of
956 these computations are performed within fractions of a second and with little conscious
957 effort in neurotypical individuals just prior to the initiation of the reach. On the basis of
958 electrophysiological recordings in non-human primates, contemporary theories of
959 visuomotor control implicate a cortical network spanning the parietal, prefrontal, and
960 occipital cortices for coding the spatial transformations that underlie goal-directed eye
961 and limb movements.

962

963 Despite DF's impairments in the perception of object size, shape, and orientation, when
964 she reaches out to pick up a goal object, her hand configures in-flight to suit the size,
965 shape, and orientation of that object [14,25,125]. The same counter-intuitive result was
966 observed in visual form agnostic patient JS, when he was tested with the same sets of
967 shapes [126]. Despite the similarity between JS and DF in terms of their perceptual
968 deficit in shape and orientation perception, JS's lesions are restricted to the
969 ventromedial occipitotemporal cortex, rather than the ventrolateral site in DF.
970 Furthermore, the published scans outlining the extent of the lesion in JS's brain strongly
971 indicate the involvement of the IFOF, ILF, or both. The involvement of the ventromedial
972 occipitotemporal cortex and its underlying white matter reinforces the viewpoint that
973 shape processing for perception engages a network of a number of different cortical
974 structures along the ventral visual pathway [34].

975

976 Consideration for the role that scale attention must play in the selection of different parts
977 of complex objects, particularly when those parts possess different functions, is also
978 important for grasping complex objects, like tools. Here, DF and HJA's grasps reveal
979 important shortcomings. For example, when reaching to pick up a hammer in order to
980 demonstrate its use to an experimenter, DF will reach for the end of the tool closest to
981 her, rather than for the handle, regardless of the hammer's orientation [127]. It is only
982 after her hand makes contact with the hammer and explores it haptically that she
983 adjusts her hand's posture to grasp the handle, before lifting the hammer up and
984 demonstrating its use successfully. Normally-sighted individuals will reach for the
985 handle, regardless of its orientation, presumably because this is the most efficient way
986 to transition from acquiring the hammer to using it. The visual nature of DF's deficit in
987 shape perception impairs her ability to use geometric form to cue semantic information
988 about what the object is and how its different parts should be used.

989

990 DF's problems with selecting object parts for grasping is also evident in her inability to
991 select the appropriate part of a 3D cross when asked to grasp and rotate it 45 degrees
992 clockwise [127]. When asked to perform this task, normally-sighted individuals adjust

993 the orientation of their grasp aperture before making contact with the cross, taking into
994 account the starting orientation of the object and its desired orientation in order to
995 minimize awkward transitional hand configurations and wrist rotations. Unlike controls,
996 DF adopts a default strategy, grasping the cross at a relatively consistent angle,
997 regardless of the cross's orientation [127]. This means she ends up grasping the
998 intersection of the cross as much as she grasps one of the bars of the cross.

999

1000 Relative to DF, HJA's visual shape perception was by and large spared, and both his
1001 grasps when directed at simple 'Efron' blocks and his performance when posting
1002 'letters' were normal [45]. Like DF, however, HJA's reaching and grasping ability was
1003 limited to simple objects, even though his perception of object shape and orientation
1004 remained largely intact. When the objects were tools that possessed parts with distinct
1005 functions, he was unable to select the appropriate part to grasp. This suggests the
1006 medial occipitotemporal cortex's involvement in the integration of semantic information
1007 for the selection of object parts for functional grasps [45].

1008

1009 DF and HJA retain a parietal pathway for the visual analysis of 3D geometry for visually-
1010 guided actions directed at objects with few distinct parts. However, while DF's lesions in
1011 the ventral cortex are localized to ventrolateral occipitotemporal cortex, HJA's lesions
1012 are confined to the ventromedial anterior occipital and temporal cortex. This suggests
1013 that the ventromedial temporal cortex plays a crucial role in scale attention for
1014 segmenting objects, particularly in cases where semantic information normally aids in
1015 the selection of appropriate object parts for grasping.

1016

1017 *Pathways underlying visual shape processing for action*

1018 The pathways that carry visual signals between visual and premotor and motor cortex
1019 are subcomponents of the three divisions of the superior longitudinal fasciculus (SLF;
1020 (see also Fig. 2). The SLF is the largest of the long association fibers that are
1021 associated with vision [128-132]. SLF-I is the dorsomedial-most of the three divisions
1022 and it interconnects the precuneus of medial posterior superior parietal lobule with
1023 medial superior frontal gyrus, premotor, and motor areas of the dorsal frontal cortex

1024 [128-132]. SLF-II is situated ventrolaterally relative to the SLF-I, interconnecting the
1025 anterior dorsolateral occipital cortex and adjacent angular gyrus in the inferior parietal
1026 lobe with the middle frontal cortex [128-132]. The SLF-III is a shorter fiber pathway that
1027 interconnects the supramarginal gyrus with the inferior frontal gyrus in the ventral frontal
1028 cortex.

1029

1030 Lesions to cortical structures in and around the anterior intraparietal sulcus (aIPS) have
1031 long been known to result in deficits in reaching for objects to pick them up, the in-flight
1032 configuration of the hand, the selection of grasp points on the target itself, and the
1033 dexterous finger movements that unfold after the hand makes contact with it [133-138].
1034 Different lines of evidence in neurotypical and normally-sighted individuals support a
1035 necessary role for the aIPS in visually-guided grasping. For example, functional-MRI
1036 activation in the aIPS of normally-sighted individuals is greater when they reach for
1037 objects to pick up using their index-finger and thumb (a 'pincer grasp') than when they
1038 merely reach for them to touch with their index-finger or knuckle [133,139-141].

1039 Moreover, transcranial magnetic stimulation (TMS) to aIPS disrupts the formation of the
1040 in-flight grasp aperture [142,143] and increases the area over the object in which the
1041 fingers first make contact [144], strongly suggesting a role for the aIPS in the selection
1042 of grasp points. Notably, the aIPS forms part of a larger, left-lateralized 'praxis network'
1043 involving the premotor cortex that is involved in the timing and sequencing of goal-
1044 oriented muscle movements [e.g., 145; for review, see 146].

1045

1046 *Visual agnosia and semantic contributions to visually-guided grasping*

1047 One open question that visual agnosia may help address is how semantic information
1048 about an object, including its use, is delivered to the visuomotor structures in the PPC
1049 and premotor cortex. When we reach out to pick up complex goal objects that are made
1050 of constituent parts that possess different functions, semantic information about the
1051 object along with shape and surface-based visual processing must be integrated into
1052 the motor plan in order to select grasp points that are suitable for using the object in its
1053 intended manner.

1054

1055 We have suggested that the vertical and posterior components of the SLF that
1056 interconnect ventral and lateral occipitotemporal cortical areas with the posterior parietal
1057 cortex might mediate direct interactions between cortical sources of semantic
1058 information about the functional parts of complex objects, like tools, and cortical sources
1059 involved in the selection of hand postures and grasp points for motor planning and
1060 execution. In line with this notion, fMRI activity in praxis network areas, including the
1061 posterior middle temporal gyrus and LOC, areas associated with the vertical SLF, are
1062 more active when viewing real tools vs. Frankenstein-like objects that are made from
1063 the parts of different tools [147]. Furthermore, dynamic causal modelling suggests fMRI
1064 activity in the LOC leads activity in aIPS when participants view pictures of tools,
1065 relative to pictures of non-tool objects that possess a similar, size, shape, and
1066 orientation [148]. Moreover, real tool use invokes fMRI activity in these same structures
1067 as well as others in the praxis network [145,149-151].

1068
1069 With a handful of noted exceptions, there are only a few detailed studies of the reach-to-
1070 grasp actions of patients with visual agnosia. This is likely because these patients often
1071 times show no obvious problem reaching for and acquiring objects. Nevertheless, as
1072 case studies of HJA and DF have shown, careful laboratory observation can reveal
1073 important impairments in the selection of suitable object parts, particularly when the
1074 selection depends on visual access to semantic, functional information about what the
1075 object is and how to use it. Quantifying patterns of deficits and spared abilities and the
1076 location and extent of neural damage allows us to test our ideas about the causal
1077 relationships between function and anatomy.

1078
1079 *Neglect and the role of object-centered attention in visually-guided grasping*

1080 A related open question concerns the role that attention plays in the construction of
1081 motor plans for goal-directed action like reaching for and grasping objects. A few
1082 studies have investigated different aspects of reaching and grasping in neglect patients.
1083 When patients with neglect are presented with an object to pick up, the path the hand
1084 takes from its initial resting position deviates towards a distractor object, provided the
1085 distractor is located on the ipsilesional side of the target [152]. Interestingly, the hand's

1086 in-flight grasp aperture remains unaffected, suggesting that neglect, and presumably
1087 selective attention to scale, can operate on different components of reaching and
1088 grasping movements, similar to the distinction between spatial (target location) and
1089 object-centered (the selection of grasp points) components of neglect.

1090
1091 Pritchard reported the results of a case of visual neglect in which the patient's
1092 perception of the size of a target object presented in the contralesional visual field was
1093 compressed relative to when the same object was presented in the ipsilesional field
1094 [153; see also 154]. Remarkably, when the patient was asked to reach for and pick up
1095 the object, her in-flight grasp aperture reflected the bar's real size regardless of whether
1096 the object was presented in the contralesional or ipsilesional field [153]. Unfortunately,
1097 detailed scans of the patient's brain were not published. Nevertheless, the authors
1098 described the site of the lesion as right occipitotemporal cortex, extending into the
1099 medial temporal lobe. The extent along the superior-inferior dimension was left
1100 unspecified. Thus, it appears that the damage spared the dorsal PPC, along with those
1101 structures around the intraparietal sulcus that are engaged when we reach for and pick-
1102 up goal objects.

1103
1104 It is also worth noting that there were other signs the patient's visual perception may
1105 have been abnormal. She could not, for example, complete the Benton visual form
1106 discrimination task [154]. This task entails matching a target 'set' of three objects
1107 against four sample sets, only one of which is identical to the target set. The remaining
1108 three foil sets contain objects that are either arranged differently with respect to one
1109 another, or some of the objects within the set differ in a subtle way from their
1110 correspondents in the target set. In short, this task strikes us as requiring selective
1111 scale-based attention, which would appear to have been severely compromised in the
1112 patient. Given the description of the lesion, it is possible that the damage to this
1113 patient's occipital and medial temporal cortex extended into the underlying white matter,
1114 which could include the ILF, IFOF, and/or the posterior, vertical segments of the SLF.
1115 Damage to these segments of the SLF would be consistent with our view that these
1116 pathways aid the operations of selective scale-based attention in the construction of the

1117 content of visual awareness. This would explain why the patient experienced a deficit in
1118 the perceived size of targets located on the left. Furthermore, the lesion did not appear
1119 to involve the PPC. Given the involvement of the PPC in visually-guided reaching and
1120 grasping, this would help explain why the patient's grasp aperture remained tuned to the
1121 real size of those same objects.

1122
1123 Marrotta and colleagues reported a study of shape discrimination and grasp point
1124 selection in six neglect patients [155]. These authors administered a test similar to the
1125 one Goodale and colleagues administered to DF, using smooth pebble-like 3D shapes
1126 [125]. In one of the conditions, the patient is presented with two of these shapes at two
1127 different locations along their midline and is asked to make a same/different judgment
1128 about their shape. On half the trials, the shapes are the same. Furthermore, the
1129 orientation of the shapes is randomly varied. The authors found that even on the shape-
1130 discrimination task, the patients performed poorly, albeit scoring above chance, and
1131 therefore better than DF, who has visual form agnosia, but well below normally-sighted
1132 controls and the right hemisphere damaged controls. In other words, these patients
1133 appeared to possess symptoms of object-centered neglect.

1134
1135 In a second condition, performed after the patient made their same/different judgment
1136 about object shape on each trial, Marotta and colleagues removed one of the shapes
1137 and then asked the patient to reach for and pick up the remaining one [155]. Due to the
1138 smooth pebble-like shape of the targets, the grasp points had to be chosen carefully to
1139 minimize instability of the resultant grip. This tends to involve selecting points for thumb
1140 and forefinger on the target's surface that result in a corresponding 'opposition axis' that
1141 lies close to the target's center of mass. For this task, the patient's finger tips were inked
1142 so that their touchpoints would leave marks on the side of the target. This way, the
1143 experimenter could record where the patient grasped the object, and then determine
1144 afterwards how close their grasp points were to the center of the target's mass, on
1145 average, across many trials. Marotta and colleagues found that the grasp points the
1146 neglect patient selected were shifted rightward, relative to those of the controls, towards
1147 the right (ipsilesional) side of the object. In fact, the extent of shift in the grasp points

1148 were correlated with the severity of neglect, as indicated by their scores on the BIT
1149 [155]. Thus, in this case it is possible that the impaired perceptual processing for shape
1150 may have also affected the selection of grasp points. Unfortunately, detailed scans of
1151 the only patient in the group with a lesion in the parietal, occipital, and temporal cortex
1152 (presumably the TPJ) were not published, and the scans that are available lack
1153 sufficient detail to draw any conclusive inferences about the relationship between lesion
1154 site and extent and performance on the two tasks.

1155

1156 *Conclusion*

1157 One of the overarching aims of this review is to propose a more prominent role for
1158 selective attention to scale in understanding the conditions of visual agnosia and
1159 neglect. Our review of this literature points to the critical role of attention to scene and
1160 object scale in the construction of the content of visual awareness and in the selection
1161 of different object parts and object-surface points for goal-directed action like grasping.
1162 Some of the strongest support for this proposal comes from a subset of visuospatial
1163 neglect patients who possess object-based deficits in attention that resemble the
1164 perceptual deficits of patients with visual agnosia, and from two heavily studied patients
1165 with visual agnosia, DF and HJA. Our interpretation is that selective attention to the
1166 appropriate structural scale of a scene facilitates effective visual perception. That is,
1167 attention to the appropriate scale helps to construct the contents of awareness,
1168 including scenes, ensembles of objects, objects themselves, and the selection of object
1169 parts for recognition and action.

1170

1171 At the same time, it is important to note that we are not claiming that behavioural and
1172 neural responses cannot be reliable in the absence of selective attention to scale.
1173 Blindsight, in which patients respond reliably to visual stimulation presented in clinically-
1174 blind fields, is a notable case in point demonstrating that selective attention to scale is
1175 not essential for successful visual-motor coordination to simple rectilinear and cylindrical
1176 shapes (e.g., 156-158). Rather, it is our view that under typical circumstances, the
1177 visual contents of immediate awareness are constructed within the occipital and inferior
1178 temporal cortices, and it is in the construction of these phenomenological

1179 representations that selective attention to scale plays a critical role. We have argued
1180 here that the origins of these attentional signals lie in parietal and frontal attentional
1181 centers. In so doing, we have highlighted the direct and indirect pathways that seem
1182 capable of delivering these signals to the inferior occipitotemporal structures that, as
1183 cases of visual agnosia have shown, are necessary for normal conscious visual
1184 experience.

1185
1186 Neuropsychological studies of visual agnosia have contributed substantially for over 100
1187 years to informing theoretical models of the structure and function of the human visual
1188 system. The most recent strides in understanding have come from the development of
1189 brain imaging techniques that permit detailed anatomical visualization as well as
1190 functional visualization while an individual is perceiving and acting. Nonetheless,
1191 detailed patient case work is still foundational, because they often guide the brain
1192 imaging that affords us more precise tests of our ideas about the structural and
1193 functional relationships. The study of visual object agnosia is central to our current
1194 understanding that the mental representation of the visible world involves a parallel
1195 interplay between visual sensory inputs, past experience, and perceptual and
1196 behavioural end-points of action.

1197
1198 In this review, we have highlighted that the tendency among researchers to study
1199 aspects of selective attention in isolation — for example, spatial attention, featural
1200 attention, and object-based attention — may have contributed to the neglect of a
1201 critically important aspect of selective attention. Specifically, selective attention to one
1202 level in the structural hierarchy of a visual scene over another. Such selection is
1203 essential for successful perception of, and action towards, objects within a given scene.
1204 Moreover, such selection always entails attention to spatial locations, features, and
1205 objects, but notably, only at the scale that is required for a given perceptual or motor
1206 task.

1207
1208 In developing this account, we have also highlighted an important area for further
1209 research — visually-guided action in visual agnosia and visual neglect — that is likely to

1210 yield theoretical insights on still-unresolved issues. Although cases of visual agnosia are
1211 quite rare, cases of neglect are relatively common following right hemispheric stroke
1212 (~44 - 48%, see 83,159). Thus, neglect, and more specifically the object-centered
1213 variant of it, might be a more accessible model to study the relationship between
1214 selective attention to scale, object perception, and visually-guided action. More work is
1215 needed to determine the conditions in which scale-based attention operates differently
1216 on the content of visual awareness than it does on visually-guided action and to
1217 determine the neural underpinnings of these processes.

1218

1219 Finally, it is worthwhile mentioning that the literature of case reports involving patients
1220 with visual agnosia, and some patients with visual neglect, is replete with brief clinical
1221 descriptive accounts of rapid partial recovery in visual function. We currently know very
1222 little about how neural rewiring in the visual system helps reestablish facets of visual
1223 perception and recognition following damage. Neuroimaging uniquely affords
1224 researchers and clinicians the tools to study this nascent field of neural plasticity in
1225 patients with compromised visual perception. Therefore, we remain optimistic that
1226 additional studies of patients with visual agnosia and patients with visual neglect will
1227 continue to yield important insights into how the brain uses vision for perception,
1228 cognition, and action.

1229

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