### Hanlin Tang and Gabriel Kreiman

Pattern recognition involves building a mental model to interpret incoming inputs. 3 This incoming information is often incomplete and the mental model must 4 extrapolate to complete the patterns, a process that is constrained by the statistical 5 regularities in nature. Examples of pattern completion involve identification of 6 objects presented under unfavorable luminance or interpretation of speech cor-rupted by acoustic noise. Pattern completion is also at the heart of other high-level 8 cognitive phenomena including our ability to discern actions from still images or to q predict behavioral patterns from observations. 10

Pattern completion constitutes a ubiquitous challenge during natural vision. 11 Stimuli are often partially occluded, or degraded by changes in illumination and 12 contrast. While much progress has been made towards understanding the mecha-13 nisms underlying recognition of complete objects, the neural computations under-14 lying more challenging recognition problems such as object occlusion remain 15 poorly understood. Here we generically refer to object occlusion to include any 16 transformation where only partial information about an object is accessible (such as 17 the multiple examples illustrated in Fig. 1), and refer to object completion as the 18 ability to infer object identity from partial information (without necessarily 19 implying that subjects perceptually fill in the missing information). 20

Understanding how the neural representations of visual signals are modified 21 when objects are occluded is critical to developing biologically constrained com-22 putational models of occluded object recognition and may also shed light on how to 23 solve manifestations of pattern completion in other domains. The development of 24 feed-forward models for visual recognition of whole objects has been driven by 25 behavioral and physiological experiments establishing the hierarchy of feature 26 tuning and robustness to image transformations. Similarly, by systematically 27 examining when and where neural representations that are robust to occlusion 28

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**Fig. 1** Object completion examples **a** Occluded geometric shape (*left*) and its mosaic counterpart (*right*) (e.g. Murray 2004). **b** Example of modal completion inducing an illusory triangle (*left*). This percept is disrupted by adding edges to the inducers (*right*). **c** Line drawing of an object defined by disconnected segments and its fragmented counterpart, similar to (e.g. Doniger et al. 2000; Sehatpour et al. 2008). **d** Line drawing of an occluded object and its scrambled counterpart (e.g. Lerner et al. 2004, 2002). **e** Occluded object and its 'deleted' counterpart (e.g. Johnson and Olshausen 2005). **f** Example partial image of an object seen through bubbles with a phase-scrambled background to equalize contrast (e.g. Tang et al. 2014). **g** Example partial image of a scene (e.g. Nielsen et al. 2006)

emerge can help extend our theoretical understanding of vision and develop the next generation of computational models in vision. Understanding pattern completion and recognition of occluded objects is a challenging task: performance depends on the stimulus complexity, the type and amount of occlusion and the task itself. In this chapter, we summarize recent efforts to examine the mechanisms underlying recognition of partially occluded objects and discuss several avenues for future work towards a theory of object completion.

## <sup>36</sup> 1 Visual System Hierarchy

Object recognition is orchestrated through a semi-hierarchical series of processing areas along ventral visual cortex (Connor et al. 2007; DiCarlo et al. 2012; Felleman and Van Essen 1991; Logothetis and Sheinberg 1996; Riesenhuber and Poggio 1999; Schmolesky et al. 1998; Tanaka 1996). At each step in this hierarchy, the

	Layout: T1 Standard STIX	Book ID: 312720_1_En	Book ISBN: 978-981-10-0211-3
Ŋ	Chapter No.: 3	Date: 11-8-2016 Time: 2:27 pm	Page: 3/18

feature specificity of the neurons increases in complexity. For example, neurons in 41 primary visual cortex (V1), respond selectively to bars of a particular orientation 42 (Hubel and Wiesel 1959) whereas neurons in inferior temporal cortex respond 43 preferentially to complex shapes including faces and other objects (Desimone et al. 44 1984; Gross et al. 1969; Perrett et al. 1992; Richmond et al. 1983; Rolls 1991). In 45 addition to this increase in feature complexity, there is a concomitant progression in 46 the degree of tolerance to object transformations such as changes in object position 47 or scale (Hung et al. 2005; Ito et al. 1995; Logothetis et al. 1995). The selective and 48 tolerant physiological responses characterized in the macaque inferior temporal 49 cortex have also been observed in the human inferior temporal cortex (Allison et al. 50 1999; Liu et al. 2009). The timing of these neural responses provides important 51 constraints on the number of possible computations involved in visual recognition. 52 Multiple lines of evidence from human psychophysical measurements (Potter and 53 Levy 1969; Thorpe et al. 1996), macaque single unit recordings (Hung et al. 2005; 54 Keysers et al. 2001), human EEG (Thorpe et al. 1996) and human intracranial 55 recordings (Allison et al. 1999; Liu et al. 2009) have established that selective 56 responses to whole objects emerge within 100-150 ms of stimulus onset in the 57 highest echelons of the ventral visual stream. 58

Research over the last several decades characterizing the spatiotemporal 59 dynamics involved in the neural representation of objects in these successive areas 60 has led to the development of a theoretical framework to explain the mechanisms 61 underlying object recognition. An influential theoretical framework suggests that, to 62 a first approximation, processing of visual information traverses through the ventral 63 stream in a feed-forward fashion, without significant contributions from long 64 top-down feedback loops or within-area recurrent computations (Deco and Rolls 65 2004; Fukushima 1980; LeCun et al. 1998; Mel 1997; Olshausen et al. 1993; 66 Riesenhuber and Poggio 1999; Wallis and Rolls 1997). Consistent with this notion, 67 computational models of object recognition instantiating feed-forward processing 68 provide a parsimonious explanation for the selectivity and tolerances observed 69 experimentally (Serre et al. 2007b). The activity of these computational units at 70 various stages of processing captures the variability in the neural representation 71 from macaque single unit recordings along the visual hierarchy (Cadieu et al. 2014; 72 Yamins et al. 2014). These feed-forward computational models have inspired the 73 development of deep convolutional networks that demonstrate a significant degree 74 of success in a variety of computer vision approaches to object recognition (e.g. 75 Hinton and Salakhutdinov 2006; LeCun et al. 1998; Russakovsky et al. 2015; Sun 76 et al. 2014; Taigman et al. 2014). 77

These purely feedforward architectures do not incorporate any feedback or 78 recurrent connections. However, at the anatomical level, feedback and recurrent 79 connections figure prominently throughout the visual system (Felleman and Van 80 Essen 1991). In fact, quantitative anatomical studies have suggested that feedback 81 and recurrent connections significantly outnumber feedforward ones (Callaway 82 2004; Douglas and Martin 2004). The computational contributions of these feed-83 back and recurrent projections are largely underexplored in existing computational 84 models of visual recognition because their underlying roles remain unclear. Several 85

investigators have suggested that these feedback and recurrent projections could
play an important role during object recognition under conditions where the visual
cues are impoverished (e.g. poor illumination, low contrast) or even partially
missing (e.g. visual occlusion) (Carpenter and Grossberg 2002; Hopfield 1982;
Mumford 1992; Tang et al. 2014; Wyatte et al. 2012a).

Following the approach suggested by Marr in his classic book on vision (Marr 92 1982), we subdivide our discussion of recognition of occluded objects into three 93 parts: (i) definition of the *computational problem* by describing behavioral per-94 formance during recognition of occluded objects, (ii) characterization of the *im-*95 *plementation at the physical level* describing the neural responses to occluded 96 objects and (iii) initial sketches of *theoretical ideas instantiated into computational* 97 *models* that aim to recognize occluded objects.

## <sup>98</sup> 2 The Computational Problem of Object Completion

Figure 1 shows examples of several images that induce object completion. In the natural world, objects can be partially occluded in multiple different ways due to the presence of explicit occluders, shadows, camouflage and differential illumination. Object completion is an ill-posed problem: in general, there are infinite ways of completing contours from partial information. The visual system must be able to infer what the object is despite the existence of all of these possible solutions consistent with the visual input.

### 106 2.1 Amodal Completion

Occluded shapes can be perceived as whole (Fig. 1a, compare left and right panels). 107 Object completion can be *amodal* when there is an explicit occluder and the subject 108 cannot see the contours behind the occluder despite being aware of the overall 109 shape (Singh 2004). In contrast, in the famous illusory triangle example (Fig. 1b), 110 Kanizsa describes the phenomenon known as modal completion whereby the object 111 is completed by inducing illusory contours that are perceived by the observer 112 (Kanizsa 1979). Because these illusory inducers are rare in natural vision, in this 113 chapter we focus on amodal completion. Even though occluded or partial objects 114 such as the ones shown in Fig. 1c, d are segmented, observers view the object as a 115 single percept, not as disjointed segments. Amodal completion is also important for 116 achieving this single `gestalt'. Investigators have used a variety of different stimuli 117 to probe the workings of object completion, ranging from simple lines and geo-118 metric shapes to naturalistic objects such as the ones shown in Fig. 1e-g. 119

Psychophysical studies of amodal completion have provided many clues to the
 underlying computations (Kellman et al. 2001; Sekuler and Murray 2001). Amodal
 completion relies on an inferred depth between the occluder shape and the occluded

ß	Layout: T1 Standard STIX	Book ID: 312720_1_1	En	Book ISBN: 978-981-10-0211-3
Ņ	Chapter No.: 3	Date: 11-8-2016	Time: 2:27 pm	Page: 5/18

object, which in turns generates a surface-based representation of the scene 123 (Nakayama et al. 1995). In fact, presence of the occluder aids in identifying the 124 occluded object, as powerfully illustrated by the Bregman's occluded B letters 125 (Bregman 1981) Grouping of different parts into a complete whole, and the 126 'completion' of missing lines and contours, represent an important component of 127 object recognition. There are infinite possible ways of completing occluded objects. 128 The ambiguities arise from the many combinations with which occluded edges. 129 called `inducers' can be paired together, as well as the infinite possible contours 130 between two pairs of inducers (Kellman et al. 2001; Nakayama et al. 1995; Ullman 131 1976). Despite the many possible solutions, the visual system typically arrives at a 132 single (and correct) interpretation of the image. 133

The temporal dynamics of shape completion can constrain the computational 134 steps involved in processing occluded images. Psychophysics experiments have 135 measured the time course of amodal completion with a diverse array of experi-136 mental paradigms. The most common method is a contrast of an occluded shape 137 against its mosaic parts (e.g. Figure 1a). For example, in the prime matching 138 paradigm, subjects are first primed with a stimulus, and then asked to judge whether 139 a pair of test stimuli represent the same or a different shape. Subjects are faster to 140 correctly respond 'same' when the primed shape is the same as the test stimuli. 141 When partly occluded objects are used as the prime, this priming effect depends on 142 the exposure time (Sekuler and Palmer 1992). At short durations (50 ms), occluded 143 objects primed subject's responses towards mosaic shapes, suggesting that 50 ms is 144 not enough time for amodal completion of the prime stimulus. At longer durations 145 (100 ms or more), the priming effect switched to favor whole shapes. Therefore, the 146 authors estimate that amodal completion for simple geometric shapes takes between 147 100 and 200 ms, depending on the amount of occlusion (Sekuler et al. 1994). 148 A different set of behavioral experiments suggests approximately the same time 149 scales for amodal completion; in several studies, subjects are asked to discriminate 150 shapes in a timed forced-choice task. Response times to occluded shapes lagged 151 those to whole shapes by about 75-150 ms (Murray et al. 2001; Shore and Enns 152 1997). For naturalistic objects such as faces, however, Chen et al. report that 153 amodal completion takes longer than 200 ms (Chen et al. 2009), well beyond the 154 previous estimates based on simpler shapes and tasks. 155

# 2.2 From Amodal Completion to Recognition of Occluded Objects

Many studies of amodal completion have used simple shapes and contours, as outlined in the previous section. When recognizing whole objects, psychophysical studies using simple shapes and neurophysiological studies describing the linear filters in primary visual areas led to the basic building blocks to develop deep models of visual recognition capable of detecting complex shapes. Inspired by the

ß	Layout: T1 Standard STIX	Book ID: 312720_1_En	Book ISBN: 978-981-10-0211-3
5	Chapter No.: 3	Date: 11-8-2016 Time: 2:27 pm	Page: 6/18





Fig. 2 Robust object categorization despite strong occlusion a Experiment timeline. Partial images similar to the ones shown in Fig. 1f were presented during exposure times ranging from 33 to 150 ms. Subjects performed a five alternative forced-choice categorization task determining whether the image contained animals, chairs, faces, fruits, or vehicles. b Performance as a function of percentage occlusion across n = 14subjects for various exposure times. Error bars denote SEM. Dashed line indicates chance performance



success of this approach, we assume that contour completion is one of the initial steps involved in interpreting complex objects that are partially occluded.

Recognition remains robust to partial occlusion for complex objects. We used 165 naturalistic objects that were occluded by presenting information through "bubbles" 166 (Gosselin and Schyns 2001) (Fig. 1f). After a variable exposure time from 33 to 167 150 ms, subjects performed a five alternative forced-choice categorization task. 168 Recognition was robust even when 80-90 % of the object was occluded across the 169 various exposure times (Fig. 2). Similar results were obtained by (Wyatte et al. 170 2012a). As illustrated by Bregman (1981), the presence of an occluder during object 171 completion aids recognition performance. For example, one study presented natural 172 objects that were either occluded (Fig. 1e, left) or where the same object parts were 173 deleted (Fig. 1e, right). Recognition was significantly impaired in the deleted part 174 case compared to the occluded part case, but only when using high percentage of 175 occlusion (>75 % missing pixels) (Johnson and Olshausen 2005). 176

Intuitively, we would expect successful recognition to depend on the exact features shown. This intuition was quantitatively measured by (Gosselin and Schyns 2001): the facial features critical to recognition varied depending on the task (e.g. the eyes and eyebrows were more relevant for gender discrimination and the mouth provided more information when evaluating expressiveness). Similar conclusions were reached when using the same paradigm to evaluate recognition in monkeys (Nielsen et al. 2006).

3	Layout: T1 Standard STIX	Book ID: 312720_1_En	В
Ś	Chapter No.: 3	Date: 11-8-2016 Time: 2:27 pm	P

Book ISBN: 978-981-10-0211-3 Page: 7/18

Recognition of Occluded Objects

## **3** Neural Representation of Occluded Objects

A series of scalp electroencephalography (EEG) studies have measured the latency 185 at which responses differ between occluded objects and suitable control images. 186 Using simple geometric stimuli, differences between occluded shapes and notched 187 shapes emerged at 140–240 ms (Murray 2004). Using more naturalistic stimuli (e.g. 188 Figure 1e), other investigators report differential activity in the 130–220 ms (Chen 189 et al. 2010) and 150-200 ms (Johnson and Olshausen 2005) ranges. In a more 190 difficult task with fragmented line drawings that are progressively completed, 191 Doniger et al. reported that differences are only observed in the 200-250 ms 192 response window. Even though these studies use different stimuli and make dif-193 ferent comparisons, they consistently conclude that amodal completion effects 194 manifest within 130-250 ms. 195

Several neuroimaging (Hegde et al. 2008; Komatsu 2006; Lerner et al. 2004, 196 2002; Olson et al. 2004; Rauschenberger et al. 2004) and scalp EEG (Chen et al. 197 2010; Doniger et al. 2000; Johnson and Olshausen 2005) studies with more com-198 plex objects have contrasted activity changes between an occluded object and an 199 appropriately scrambled counterpart (e.g. Fig. 1c, d). In these stimuli, the low-level 200 features are maintained but disruption in their geometric arrangement destroys the 201 percept. For example, investigators have reported differential activity in the 202 lateral-occipital complex between occluded line drawings and their scrambled 203 counterparts (Lerner et al. 2002). The authors reason that, since the occluded 204 images elicit a larger response in the lateral-occipital complex (LOC) than scram-205 bled images, the LOC could be involved in object completion. It should be noted 206 that LOC also demonstrates increased activity to whole objects compared to 207 scrambled versions of those objects without any occlusion (Grill-Spector et al. 208 2001). Thus, the increased responses to whole objects may not be necessarily 209 related to object completion mechanisms per se, but rather neural activity related to 210 perceptual recognition. 211

Similarly, EEG and intracranial studies compared line drawings against their 212 fragmented counterparts (Doniger et al. 2000; Sehatpour et al. 2008) to measure the 213 timing and brain regions involved in object completion. Schatpour et al. worked 214 with epilepsy patients who have intracranial electrodes implanted for clinical pur-215 poses. This approach allows a rare opportunity to record directly from human brain. 216 The authors take advantage of simultaneous recordings from multiple brain regions 217 to show that line fragments elicited greater coherence in the LOC-Prefrontal 218 Cortex-Hippocampus network compared to scrambled line fragments. They suggest 219 that this network synchrony is responsible for the perceptual line closure of objects. 220 In order to understand the neural mechanisms orchestrating object completion, it 221 is also critical to examine the neural architectures that could implement the com-222 putational solutions suggested in the previous section. Essential aspects of object 223 completion can be traced back to the earliest stages in visual processing. An early 224 study demonstrated that neurons in area V2 show selective responses to illusory 225 contours (Peterhans and von der Heydt 1991; von der Heydt et al. 1984). Other 226

9	Layout: T1 Standard STIX	Book ID: 312720_1_En	Book ISBN: 978-981-10-0211-3
5	Chapter No.: 3	Date: 11-8-2016 Time: 2:27 pm	Page: 8/18

work has demonstrated that even V1 neurons can respond to occluded shapes. One 227 study recorded single cells in macaque V1 when presented with occluded moving 228 bars (Sugita 1999). Approximately 12 % of orientation-selective cells responded to 229 the moving oriented bar even when it was occluded, thus potentially underlying the 230 phenomenology of amodal completion. These cells responded strongly only when 231 the occluder was presented in front of the moving bar (positive disparity), and not at 232 zero or negative disparity. Notably, responses to the occluded bar were not different 233 from those obtained when presenting the bar alone. These results have led to the 234 suggestion that amodal completion is achieved by contextual modulation from 235 outside the classical receptive field. While other studies have suggested that con-236 textual modulation occurs with a delay of 50-70 ms with respect to the onset of the 237 visually evoked responses (Bakin et al. 2000; Zipser et al. 1996), Sugita did not 238 observe any latency delays for the amodally-completed response. The author sug-239 gests that these contextual modulations may come from lateral connections or 240 feedback from proximal areas. In another study, responses to illusory contours in 241 V1 were delayed by about 55 ms compared to the response to real contours (Lee 242 and Nguyen 2001). Importantly, illusory contour responses appeared first in V2 243 before emerging in V1, suggesting that modal completion in V1 might require 244 feedback modulation from V2. Complementing these studies, psychophysical 245 studies on the effect of inferred depth and apparent motion on the perception of 246 occluded surfaces also conclude that amodal completion effects manifests in early 247 visual processing (Shimojo and Nakayama 1990a, b). 248

These neurophysiology studies have focused on the occlusion or inducing of linear contours, where the inducers are close in proximity to the classical receptive field. However in natural vision we complete curvilinear contours over distances much longer than the width of classical V1 receptive fields. Often in these cases, correct completion of an object depends on the global context in which the object is embedded. Future studies are needed to examine whether and when V1 neurons respond to completed contours of varying curvature, length, and context.

As outlined above, V1 neurons feed onto a cascade of semi-hierarchical pro-256 cessing steps through V2 and V4, culminating in the inferior temporal cortex 257 (ITC) (Felleman and Van Essen 1991). How do these higher visual areas respond to 258 occluded shapes? Few studies have examined the responses in intermediate visual 259 areas to occluded shapes. A recent elegant study has begun to fill in this gap by 260 characterizing how macaque V4 neurons respond to different curvatures when they 261 are partially occluded by dots (Kosai et al. 2014). The authors report that neurons 262 can maintain selectivity within a range of occlusion. While the response onset times 263 of these neurons were not delayed by occlusion, the latency at which selectivity 264 arose was delayed by hundreds of milliseconds. 265

Kovacs et al. found that visually selective responses to complex shapes in ITC were similar between whole shapes and occluded shapes defined by adding noise, occluders or deleting shape parts (Kovács et al. 1995). Although selectivity to complex shapes was retained despite up to  $\sim$ 50 % occlusion, the absolute magnitude of the responses was modulated linearly with the amount of occlusion. Contrary to what Kosai et al. found in V4, these authors observed delays of up to 50 ms

ß	Layout: T1 Standard STIX	Book ID: 312720_1	En	Book ISBN: 978-981-10-0211-3
2	Chapter No.: 3	Date: 11-8-2016	Time: 2:27 pm	Page: 9/18

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272

in the response latency of occluded shapes. While it is tempting to attribute this discrepancy to differences in processing between V4 and IT, we note that the 273 stimuli and occluding patterns used are different between the two studies. 274

Nielsen et al. extended this work by examining the responses of IT neurons to 275 occluded objects embedded in naturalistic stimuli (Fig. 1f) (Nielsen et al. 2006a). 276 Using the bubbles paradigm (Gosselin and Schyns 2001), the authors defined parts 277 of an image that provided more diagnostic value (i.e. provided information that 278 aided recognition) versus other non-diagnostic parts. The authors first demonstrated 279 that monkeys and humans show striking behavioral similarities in terms of what 280 object parts are considered diagnostic (Nielsen et al. 2006b). For occluded scenes 281 containing diagnostic parts, both firing rates and local field potentials in ITC 282 remained largely invariant to significant amounts of occlusion, in contrast to the 283 findings of the Kovacs study with simpler stimuli (Kovacs et al. 1995). However, 284 for scenes that contained only non-diagnostic parts, the results from the Kovacs 285 study were reproduced-the firing rate varied linearly with the amount of occlusion. 286 This comparison also serves as a cautionary tale against extrapolating results based 287 on geometric shapes to the processing of more naturalistic stimuli because the 288 details of which features are revealed can play a very important role in dictating the 289 effects of occlusion. Issa et al. reached similar conclusions when demonstrating that 290 ITC responses selective to faces were particularly sensitive to occlusion of certain 201 parts (one eye) and that those parts could drive the responses almost as well as the 292 whole face (Issa and Dicarlo 2012). These results suggest that the robustness of the 293 neural representation to missing parts depends on the diagnosticity of the visible 294 features. 295

Tang et al. used intracranial recordings to evaluate how and when visually 296 selective responses to occluded objects emerge. Naturalistic objects were presented 297 through the bubbles paradigm (Gosselin and Schyns 2001) in a task similar to the 298 one illustrated in Fig. 2. The use of objects seen through bubbles evaluates the core 299 ability to spatially integrate multiple parts to subserve recognition. Figure 3 (left) 300 shows the responses from an example electrode in the fusiform gyrus that displayed 301 a strong response to face stimuli. Remarkably, the electrode showed similar 302 responses to images that displayed only  $\sim 11$  % of the object content (Fig. 3, col-303 umns 2-6). Even in cases where the images shared essentially no common pixel 304 (e.g. columns 3 and 5), the responses remained similar. Overall, the magnitude of 305 the responses did not vary with the amount of visible pixels. Yet, the responses to 306 occluded shapes were not identical to those obtained upon presenting whole ima-307 ges. A notable difference was that the responses to occluded objects were signifi-308 cantly delayed (compare the position of the arrows in Fig. 3). Selective neural 309 response emerged with a delay of ~100 ms. These delays were also apparent when 310 using a machine learning approach to decode the category or identity of the objects 311 from the physiological responses to the whole or occluded images (Fig. 4). 312

Image processing does not end with visual cortex. Information from visual 313 cortex is conveyed to frontal cortex and to medial temporal lobe structures 314 including the amygdala, hippocampus and entorhinal cortex. One group recorded 315 single unit activity in the amygdala of human epilepsy patients, and found that 316



**Fig. 3** Physiological responses in the human fusiform gyrus show tolerance to strong occlusion. Invasive intracranial field potential recordings from an electrode in the fusiform gyrus in a subject with epilepsy (modified from Tang et al. 2014). This electrode responded selectively to faces (*left*, gray = individual trials, green = average of 9 repetitions). The other panels show single trial responses to five partial images of the face. *Black bar* indicates stimulus presentation time (150 ms). Despite heavy occlusion (89 %), the neural responses to partial images were significantly delayed. The *arrow* indicates latency of the response peak with respect to image onset



neurons were surprisingly sensitive to even small degrees of occlusion (Rutishauser
et al. 2011). Their firing rates varied non-linearly with the amount of occlusion and
the responses to image parts did not necessarily bear a resemblance to the responses
to the whole images. These non-visual medial temporal lobe neurons, in effect,
'lost' the robustness developed in the ventral visual stream, in that individual parts
were not sufficient to drive the response to the level observed for whole faces.

In addition to the type of spatial integration demonstrated in the studies above, the visual system is able to integrate information over time. Temporal integration is particularly prominent in examples of action recognition. Yet, in some cases, different parts of the same object may appear in a dynamic fashion over time. At the

9	Layout: T1 Standard STIX	Book ID: 312720_1_Er	I	Book ISBN: 978-981-10-0211-3
Ņ	Chapter No.: 3	Date: 11-8-2016 Ti	.me: 2:27 pm	Page: 11/18

Recognition of Occluded Objects

behavioral level, presenting object parts asynchronously significantly disrupts object recognition performance, even when the temporal lag is as short as 16 ms 328 (Singer and Kreiman 2014). This disruption by asynchronous presentation is also 329 evident at the physiological level (Singer et al. 2015). Thus, the ability to spatially 330 integrate parts into a whole for recognition is quite sensitive to deviations from the synchronous presentation of those parts.

In sum, early visual areas show evidence of contour completion in the presence 333 of both occluded and illusory contours when the corresponding edges are in close 334 spatial proximity. In some, but not all cases, these contour completion responses 335 show a delay with respect to both responses to real contours and responses in higher 336 visual areas. In higher visual areas responsible for object recognition, physiological 337 signals show strong robustness to large degrees of occlusion, consistent with 338 behavioral recognition performance, and these physiological signals also show a 339 significant delay. The robustness in the physiological responses and the dynamic 340 delays are consistent with the behavioral observations. These delays are interpreted 341 as originating from the involvement of recurrent and/or top-down connections 342 during the process of object completion. Given these initial steps in understanding 343 plausible neural circuits underlying recognition of occluded objects, we turn our 344 attention to describing the possible biological algorithms instantiated by these 345 neural signals. 346

#### **Computational Models of Occluded Object Recognition** 4 347

There has been significant progress over the last decade in developing computa-348 tional models of object recognition (Deco and Rolls 2004; DiCarlo et al. 2012; 349 Kreiman 2013; Riesenhuber and Poggio 1999; Serre et al. 2007a). To a first 350 approximation, these models propose a hierarchical sequence of linear filtering and 351 non-linear max operations inspired by the basic principles giving rise to simple and 352 complex cells in primary visual cortex (Hubel and Wiesel 1962). Concatenating 353 multiple such operations gave rise to some of the initial models for object recog-354 nition (Fukushima 1980). Recently, these ideas have also seen wide adoption in the 355 computer science literature in the form of deep convolutional neural networks (e.g. 356 (Krizhevsky et al. 2012) among many others). Both biologically inspired models 357 and deep convolutional neural networks (CNNs) geared towards performance on 358 benchmark datasets share similar core architectures. 359

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## 4.1 Performance of Feed-Forward Models in Recognizing Occluded Objects

Time: 2:27 pm

The canonical steps in feed-forward computational models is inspired by the 362 observation of simple and complex cells in primary visual cortex of anesthetized 363 cats. In their classic study, Hubel and Wiesel discovered 'simple' cells tuned to bars 364 oriented at a particular orientation (Hubel and Wiesel 1959). They also described 365 complex' cells, which were also tuned to a preferred orientation, but exhibited a 366 degree of tolerance to the spatial translation of the stimulus. They hypothesized that 367 to generate this spatial invariance, the complex cells pool over simple cells whose 368 receptive files tile the visual space with a max-like operation. This complex cell 369 would then respond to an oriented bar regardless of its spatial location. Both 370 hierarchical models of biological vision such as HMAX (Riesenhuber and Poggio 371 1999; Serre et al. 2007b) and CNNs are composed of alternating layers of tuning 372 and pooling with increasingly more complicated tuning functions as one ascends 373 this hierarchy. Whereas biologically-inspired models such as HMAX have about 4 374 layers, state-of-the-art computer vision models have moved to complex topologies 375 with up to 20 layers and different mixtures of tuning and pooling layers (e.g. 376 Russakovsky et al. 2015). Performance of feed-forward models such as HMAX on 377 object recognition datasets match the pattern of human performance (Serre et al. 378 2007b). Additionally, the activity of individual layers in deep learning networks can 379 capture the variance of neurons in the corresponding layers in macaque cortex 380 (Cadieu et al. 2014; Yamins et al. 2014). 381

While these feed-forward architectures are designed to build tolerance to image 382 transformations such as position and scale changes, they are not necessarily robust 383 to the removal or occlusion of object features. Indeed, Fig. 5 shows the perfor-384 mance of an HMAX-like architecture in recognizing the same occluded objects 385 form Figs. 2, 3 and 4. Small amounts of occlusion do not impair performance. 386 However, performance drops rapidly with increasing occlusion, much more rapidly 387 than human performance (see "behavior" line in Fig. 5 and compare Fig. 2 versus 388 Fig. 5. Experimental simulations with other similar models confirm that that both 389 HMAX and CNN models are challenged by recognition of occluded objects (Pepik 390 et al. 2015; Wyatte et al. 2012b). Unlike position or scale transformations, the 391 underlying representation in these models is not robust to occlusion. Feed-forward 392 networks do not have explicit mechanisms to compensate for the missing features 393 of occluded objects. In addition, because these models do not distinguish between 394 the occluder and the object, the occluder can introduce spurious features that, 395 through spatial pooling, are mixed with the object features. With small amounts of 396 occlusion, the remaining features may be sufficient to lead to successful classifi-397 cation. However, with increasing levels of occlusion, the lack of sufficient infor-398 mation and completion mechanisms lead to a significant impairment in 399 performance. 400

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#### Recognition of Occluded Objects



**Fig. 5** Challenge to feed-forward computational models Performance of a hierarchical feed-forward model of biological vision (Serre et al. 2007) on recognition of partial images similar to the one shown in Fig. 1f. *Dashed line* indicates chance level. Performance (*red line*) of the model is well below that of human subjects (*solid black line*) for heavy occlusion. Span of the *black line* indicates the range of difficulty tested for humans

## 401 4.2 Beyond Feed-Forward Models

Models that incorporate additional computations beyond feed-forward architectures can be subdivided into several categories. A group of computational models describes the process by which contours are amodally completed (Ullman 1976; Yuille and Kersten 2006). These models typically rely on an axiomatic set of desirable qualities that completed curves must satisfy (such as minimum total bending energy).

Another set of ideas argues that creating an understanding of the surfaces in a scene is critical to object recognition for occluded objects. Nakayama (1995) proposes a theory where surface representation is constructed via feedback in early visual cortex by learning associations between a viewed image and the underlying surface representations. The authors argue that this intermediate surface representation is vital for subsequent recognition for occluded objects and mediates many important functions in texture segregation and visual search.

A different model proposes that neural representations of surfaces are created in three stages based on the low-level features (Sajda and Finkel 1995). First, points belonging to the same contour are bound together, followed by a process that determines the surfaces, and finally the surfaces are ordered by depth. Both feed-forward and feedback connections subserve to communicate between these three stages.

9	Layout: T1 Standard STIX	Book ID: 312720_1	L_En	Book ISBN: 978-981-10-0211-3
2	Chapter No.: 3	Date: 11-8-2016	Time: 2:27 pm	Page: 14/18

Several theories based on the role of feedback connections emphasize inference, 421 but these ideas have largely not been operationalized into object recognition 422 models. Predictive coding models are generative models of object recognition (Rao 423 and Ballard 1999). In these models, higher visual areas send their predictions to 424 lower levels, which then return only the mismatch between the predicted activity 425 and the actual activity. This creates an efficient system where each layer only sends 426 forwards signals that deviate from the receiving layer's predictions. The higher 427 layers then attempt to generate the correct hypothesis of the image by reducing the 428 incoming prediction errors. A related model proposes that visual cortex is essen-429 tially performing Bayesian inference where feed-forward inputs combine with 430 top-down priors for recognition (Lee and Mumford 2003; Yuille and Kersten 2006). 431

As pointed out by (Wyatte et al. 2014), predictive coding models would expect occluded images to lead to increased activity in visual cortex, since the first generated hypotheses would have a very large prediction errors due to occlusion. Over time, we would expect this activity to subside as the system converged on an accurate hypothesis. Neurophysiological studies, however, find decreased or unchanged activity throughout visual cortex (Kovacs et al. 1995; Nielsen et al. 2006a; Tang et al. 2014).

Several models that more directly examine object recognition deal with recog-439 nition from partial information, and do not incorporate any of the amodal com-440 pletion mechanisms previously described. These models take advantage of the 441 extensive feedback and recurrent connections in visual cortex. While the role of 442 these connections in attentional modulation has been extensively studied, their 443 contribution to object recognition remains unclear. A particularly prominent and 444 attractive class of models that can perform pattern completion is the all-to-all 445 connectivity architectures such as Hopfield networks (Hopfield 1982). The Hopfield 446 network generates attractors for previously learned patterns in such a way that if the 447 network is initialized with partial information, it can dynamically evolve towards 448 the right attractor. Interestingly, this type of dynamical convergence towards the 449 attractor state could account for the type of delays observed in the behavioral and 450 physiological experiments. This general principle is operationalized by a neural 451 network model that combines bottom-up input with top-down signals carrying 452 previously learned patterns to complete occluded objects (Fukushima 2005). For 453 occluded patterns that are novel, this network attempts to interpolate from visible 454 edges. The author applies this model to complete occluded letters of the alphabet. 455 This concept has been extended to naturalistic objects with a feed-forward model 456 that is augmented with recurrent feedback (Wyatte et al. 2012a). This recurrent 457 feedback served to strengthen the feed-forward signals that were diminished from 458 the occluded image. 459

Given that strong behavioral and neurophysiological evidence exists for amodal completion in human brain, and that surface representations are important for organizing the visual scene, theories of object recognition would be remiss to exclude these features in favor of purely feature-based recognition. An important step towards models that fully capture natural biological vision would be to integrate traditional feed-forward models with feedback mechanisms, including amodal

6	Layout: T1 Standard STIX	Book ID: 312720_1_En	Book ISBN: 978-981-10-0211-3
Ŋ	Chapter No.: 3	Date: 11-8-2016 Time: 2:27 p	m Page: 15/18

completion, surface generation, and top-down modulation based on priors and context. The challenge of recognizing occluded objects stands as the first test of these future integrative theories.

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### 469 **References**

- Allison T, Puce A, Spencer D, McCarthy G (1999) Electrophysiological studies of human face
   perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli.
   Cereb Cortex 9:415–430
- Bakin JS, Nakayama K, Gilbert CD (2000) Visual responses in monkey areas V1 and V2 to
   three-dimensional surface configurations. J Neurosci Off J Soc Neurosci 20:8188–8198
- Bregman AS (1981) Asking the 'What for'question in auditory perception. In: Perceptual
   organization, pp 99–118
- 477 Cadieu CF, Hong H, Yamins DLK, Pinto N, Ardila D, Solomon EA, Majaj NJ, DiCarlo JJ (2014)
   478 Deep neural networks rival the representation of primate IT cortex for core visual object
   479 recognition. PLoS Comput Biol 10:e1003963
- Callaway EM (2004) Feedforward, feedback and inhibitory connections in primate visual cortex.
   Neural Netw 17:625–632
- Carpenter G, Grossberg S (2002) Adaptive resonance theory. In: The handbook of brain theory and neural networks. MIT Press, Cambridge
- Chen J, Liu B, Chen B, Fang F (2009) Time course of amodal completion in face perception. Vis
   Res 49:752–758
- Chen J, Zhou T, Yang H, Fang F (2010) Cortical dynamics underlying face completion in human
   visual system. J Neurosci Off J Soc Neurosci 30:16692–16698
- Connor CE, Brincat SL, Pasupathy A (2007) Transformation of shape information in the ventral
   pathway. Curr Opin Neurobiol 17:140–147
- 490 Deco G, Rolls ET (2004) A neurodynamical cortical model of visual attention and invariant object
   491 recognition. Vis Res 44:621–642
- Desimone R, Albright T, Gross C, Bruce C (1984) Stimulus-selective properties of inferior
   temporal neurons in the macaque. J Neurosci 4:2051–2062
- 494 DiCarlo JJ, Zoccolan D, Rust NC (2012) How does the brain solve visual object recognition?
   495 Neuron 73:415–434
- 496 Doniger GM, Foxe JJ, Murray MM, Higgins BA, Snodgrass JG, Schroeder CE, Javitt DC (2000)
   Activation timecourse of ventral visual stream object-recognition areas: high density electrical
   498 mapping of perceptual closure processes. J Cogn Neurosci 12:615–621
- Douglas RJ, Martin KA (2004) Neuronal circuits of the neocortex. Annu Rev Neurosci
   27:419–451
- Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47
- Fukushima K (1980) Neocognitron: a self organizing neural network model for a mechanism of
   pattern recognition unaffected by shift in position. Biol Cybern 36:193–202
- Fukushima K (2005) Restoring partly occluded patterns: a neural network model. Neural Netw 18:33–43
- Gosselin F, Schyns PG (2001) Bubbles: a technique to reveal the use of information in recognition
   tasks. Vis Res 41:2261–2271
- Grill-Spector K, Kourtzi Z, Kanwisher N (2001) The lateral occipital complex and its role in object
   recognition. Vis Res 41:1409–1422
- Gross C, Bender D, Rocha-Miranda C (1969) Visual receptive fields of neurons in inferotemporal
- cortex of the monkey. Science 166:1303–1306

466

467

9	Layout: T1 Standard STIX	Book ID: 312720_1_En	Book ISBN: 978-981-10-0211-3
١Ş	Chapter No.: 3	Date: 11-8-2016 Time: 2:27 pm	Page: 16/18

H. Tang and G. Kreiman

Hegde J, Fang F, Murray S, Kersten D (2008) Preferential responses to occluded objects in the 513 514 human visual cortex. J Vis 8:1-16 515

16

- Hinton GE, Salakhutdinov RR (2006) Reducing the dimensionality of data with neural networks. Science 313:504–507
- Hopfield JJ (1982) Neural networks and physical systems with emergent collective computational abilities. PNAS 79:2554-2558
- Hubel D, Wiesel T (1959) Receptive fields of single neurons in the cat's striate cortex. J Physiol 519 (Lond) 148:574-591 520
- Hubel DH, Wiesel TN (1962) Receptive fields, binocular interaction and functional architecture in 521 the cat's visual cortex. J Physiol 160:106-154 522
- Hung C, Kreiman G, Poggio T, DiCarlo J (2005) Fast read-out of object identity from macaque 523 inferior temporal cortex. Science 310:863-866 524
- Issa EB, Dicarlo JJ (2012) Precedence of the eye region in neural processing of faces. J Neurosci 525 Off J Soc Neurosci 32:16666-16682 526
- Ito M, Tamura H, Fujita I, Tanaka K (1995) Size and position invariance of neuronal responses in 527 monkey inferotemporal cortex. J Neurophysiol 73:218-226 528
- Johnson JS, Olshausen BA (2005) The recognition of partially visible natural objects in the 529 presence and absence of their occluders. Vis Res 45:3262-3276 530
- Kanizsa G (1979) Organization in vision: essays on gestalt perception. Praeger Publishers 531
- Kellman PJ, Guttman SE, Wickens TD (2001) Geometric and neural models of object. In: From 532 533 fragments to objects: segmentation and grouping in vision, vol 130, p 183
- Keysers C, Xiao DK, Foldiak P, Perret DI (2001) The speed of sight. J Cogn Neurosci 13:90-101 534
- Komatsu H (2006) The neural mechanisms of perceptual filling-in. Nat Rev Neurosci 7:220-231 535
- Kosai Y, El-Shamayleh Y, Fyall AM, Pasupathy A (2014) The role of visual area V4 in the 536 discrimination of partially occluded shapes. J Neurosci Off J Soc Neurosci 34:8570-8584 537
- Kovács G, Vogels R, Orban GA (1995) Selectivity of macaque inferior temporal neurons for 538 partially occluded shapes. J Neurosci Off J Soc Neurosci 15:1984-1997 539
- Kreiman G (2013) Computational models of visual object recognition. In: Panzeri S, Quian 540 Quiroga R (eds) Principles of neural coding. Taylor and Fracis Group 541
- Krizhevsky A, Sutskever I, Hinton GE (2012) Imagenet classification with deep convolutional 542 neural networks. In: Advances in neural information processing systems, pp 1097-1105 543
- LeCun Y, Bottou L, Bengio Y, Haffner P (1998) Gradient-based learning applied to document 544 recognition. Proc IEEE 86:2278-2324 545
- Lee TS, Mumford D (2003) Hierarchical Bayesian inference in the visual cortex. J Opt Soc Am A 546 Opt Image Sci Vis 20:1434–1448 547
- Lee TS, Nguyen M (2001) Dynamics of subjective contour formation in the early visual cortex. 548 Proc Natl Acad Sci USA 98:1907-1911 549
- Lerner Y, Harel M, Malach R (2004) Rapid completion effects in human high-order visual areas. 550 Neuroimage 21:516-526 551
- Lerner Y, Hendler T, Malach R (2002) Object-completion effects in the human lateral occipital 552 complex. Cereb Cortex 12:163-177 553
- Liu H, Agam Y, Madsen JR, Kreiman G (2009) Timing, timing, timing: fast decoding of object 554 information from intracranial field potentials in human visual cortex. Neuron 62:281-290 555
- Logothetis NK, Pauls J, Poggio T (1995) Shape representation in the inferior temporal cortex of 556 monkeys. Curr Biol 5:552-563 557
- 558 Logothetis NK, Sheinberg DL (1996) Visual object recognition. Annu Rev Neurosci 19:577–621
- Marr D (1982) Vision. Freeman Publishers, San Francisco 559
- 560 Mel B (1997) SEEMORE: combining color, shape and texture histogramming in a neurally inspired approach to visual object recognition. Neural Comput 9:777 561
- Mumford D (1992) On the computational architecture of the neocortex. II. The role of 562 cortico-cortical loops. Biol Cybern 66:241-251 563
- Murray MM (2004) Setting boundaries: brain dynamics of modal and amodal illusory shape 564 completion in humans. J Neurosci 24:6898-6903 565

516

517

3	Layout: T1 Standard STIX	Book ID: 312720_	1_En	Book ISBN: 978-981-10-0211-3
5	Chapter No.: 3	Date: 11-8-2016	Time: 2:27 pm	Page: 17/18

- Murray RF, Sekuler AB, Bennett PJ (2001) Time course of amodal completion revealed by a shape discrimination task. Psychon Bull Rev 8:713–720
- Nakayama K, He Z, Shimojo S (1995) Visual surface representation: a critical link between lower-level and higher-level vision. In: Kosslyn S, Osherson D (eds) Visual cognition. The MIT Press, Cambridge
- Nielsen K, Logothetis N, Rainer G (2006a) Dissociation between LFP and spiking activity in macaque inferior temporal cortex reveals diagnostic parts-based encoding of complex objects. J Neurosci 26:9639–9645
- Nielsen KJ, Logothetis NK, Rainer G (2006b) Discrimination strategies of humans and rhesus
   monkeys for complex visual displays. Curr Biol CB 16:814–820
- Olshausen BA, Anderson CH, Van Essen DC (1993) A neurobiological model of visual attention
   and invariant pattern recognition based on dynamic routing of information. J Neurosci Off J
   Soc Neurosci 13:4700–4719
- Olson IR, Gatenby JC, Leung HC, Skudlarski P, Gore JC (2004) Neuronal representation of
   occluded objects in the human brain. Neuropsychologia 42:95–104
- Pepik B, Benenson R, Ritschel T, Schiele B (2015) What is holding back convnets for detection?
   arXiv:150802844
- Perrett D, Hietanen J, Oeam M, Benson P (1992) Organization and functions of cells responsive to
   faces in the temporal cortex. Phil Trans Roy Soc 355:23–30
- Peterhans E, von der Heydt R (1991) Subjective contours bridging the gap between
   psychophysics and physiology. Trends Neurosci 14:112–119
- Potter M, Levy E (1969) Recognition memory for a rapid sequence of pictures. J Exp Psychol 81:10–15
- Rao RP, Ballard DH (1999) Predictive coding in the visual cortex: a functional interpretation of
   some extra-classical receptive-field effects. Nat Neurosci 2:79–87
- Rauschenberger R, Peterson MA, Mosca F, Bruno N (2004) Amodal completion in visual search:
   preemption or context effects? Psychol Sci 15:351–355
- Richmond B, Wurtz R, Sato T (1983) Visual responses in inferior temporal neurons in awake
   Rhesus monkey. J Neurophysiol 50:1415–1432
- Riesenhuber M, Poggio T (1999) Hierarchical models of object recognition in cortex. Nat
   Neurosci 2:1019–1025
- <sup>597</sup> Rolls E (1991) Neural organization of higher visual functions. Curr Opin Neurobiol 1:274–278
- Russakovsky O, Deng J, Su H, Krause J, Satheesh S, Ma S, Huang Z, Karpathy A, Khosla A,
   Bernstein M et al (2015). Imagenet large scale visual recognition challenge. Int J Comput Vis
- Rutishauser U, Tudusciuc O, Neumann D, Mamelak AN, Heller AC, Ross IB, Philpott L,
   Sutherling WW, Adolphs R (2011) Single-unit responses selective for whole faces in the
   human amygdala. Curr Biol CB 21:1654–1660
- Sajda P, Finkel LH (1995) Intermediate-level visual representations and the construction of surface
   perception. J Cogn Neurosci 7:267–291
- Schmolesky M, Wang Y, Hanes D, Thompson K, Leutgeb S, Schall J, Leventhal A (1998) Signal
   timing across the macaque visual system. J Neurophysiol 79:3272–3278
- Sehatpour P, Molholm S, Schwartz TH, Mahoney JR, Mehta AD, Javitt DC, Stanton PK, Foxe JJ
   (2008) A human intracranial study of long-range oscillatory coherence across a
   frontal-occipital-hippocampal brain network during visual object processing. Proc Natl Acad
   Sci USA 105:4399–4404
- Sekuler AB, Murray RF (2001) Amodal completion: a case study in grouping. Advances in
   Psychology 130:265–293
- Sekuler AB, Palmer SE (1992) Perception of partly occluded objects: a microgenetic analysis.
   J Exp Psychol Gen 121:95–111
- Sekuler AB, Palmer SE, Flynn C (1994) Local and global processes in visual completion. Psychol
   Sci 5:260–267
- 617 Serre T, Kreiman G, Kouh M, Cadieu C, Knoblich U, Poggio T (2007a) A quantitative theory of
- 618 immediate visual recognition. Prog Brain Res 165C:33–56

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	Layout: T1 Standard STIX	Book ID: 312720_1	En	Book ISBN: 978-981-10-0211-3
2	Chapter No.: 3	Date: 11-8-2016	Time: 2:27 pm	Page: 18/18

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626

Serre T, Oliva A, Poggio T (2007b) Feedforward theories of visual cortex account for human performance in rapid categorization. PNAS 104:6424–6429

Shimojo S, Nakayama K (1990a) Amodal representation of occluded surfaces: role of invisible stimuli in apparent motion correspondence. Perception 19:285–299

- Shimojo S, Nakayama K (1990b) Real world occlusion constraints and binocular rivalry. Vis Res 30:69–80
- Shore DI, Enns JT (1997) Shape completion time depends on the size of the occluded region. J Exp Psychol Hum Percept Perform 23:980–998
- Singer JM, Kreiman G (2014) Short temporal asynchrony disrupts visual object recognition. J Vis
   14:7
- Singer JM, Madsen JR, Anderson WS, Kreiman G (2015) Sensitivity to timing and order in human
   visual cortex. J Neurophysiol 113:1656–1669
- 631 Singh M (2004) Modal and amodal completion generate different shapes. Psychol Sci 15:454–459

<sup>632</sup> Sugita Y (1999) Grouping of image fragments in primary visual cortex. Nature 401:269–272

- Sun Y, Wang X, Tang X (2014) Deeply learned face representations are sparse, selective, and
   robust. arXiv:14121265
- Taigman Y, Yang M, Ranzato MA, Wolf L (2014) Deepface: closing the gap to human-level
   performance in face verification. In: 2014 IEEE conference on computer vision and pattern
   recognition (CVPR), pp. 1701–1708. IEEE
- Tanaka K (1996) Inferotemporal cortex and object vision. Annu Rev Neurosci 19:109–139
- Tang H, Buia C, Madhavan R, Crone NE, Madsen JR, Anderson WS, Kreiman G (2014)
   Spatiotemporal dynamics underlying object completion in human ventral visual cortex. Neuron
   83:736–748
- Thorpe S, Fize D, Marlot C (1996) Speed of processing in the human visual system. Nature 381:520–522
- Ullman S (1976) Filling-in the gaps: the shape of subjective contours and a model for their generation. Biol Cybern 25:1–6
- von der Heydt R, Peterhans E, Baumgartner G (1984) Illusory contours and cortical neuron
   responses. Science 224:1260–1262
- Wallis G, Rolls ET (1997) Invariant face and object recognition in the visual system. Prog
   Neurobiol 51:167–194
- Wyatte D, Curran T, O'Reilly R (2012a) The limits of feedforward vision: recurrent processing
   promotes robust object recognition when objects are degraded. J Cogn Neurosci 24:2248–2261
- Wyatte D, Jilk DJ, O'Reilly RC (2014) Early recurrent feedback facilitates visual object
   recognition under challenging conditions. Front Psychol 5:674
- Wyatte D, Tang H, Buia C, Madsen J, O'Reilly R, Kreiman G (2012b) Object completion along
   the ventral visual stream: neural signatures and computational mechanisms. In: Computation
   and systems neuroscience, Salt Lake City, Utah
- Yamins DLK, Hong H, Cadieu CF, Solomon EA, Seibert D, DiCarlo JJ (2014)
   Performance-optimized hierarchical models predict neural responses in higher visual cortex.
   Proc Natl Acad Sci USA 111:8619–8624
- Yuille A, Kersten D (2006) Vision as Bayesian inference: analysis by synthesis? Trends Cogn Sci
   10:301–308
- Zipser K, Lamme VA, Schiller PH (1996) Contextual modulation in primary visual cortex.
   J Neurosci 16:7376–7389

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