

1 **Seeing the invisible: The scope and limits of unconscious processing**
2 **in binocular rivalry**

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Abstract

When an image is presented to one eye and a very different image is presented to the corresponding location of the other eye, they compete for conscious representation, such that only one image is visible at a time while the other is suppressed. Called binocular rivalry, this phenomenon and its deviants have been extensively exploited to study the mechanism and neural correlates of consciousness. In this paper, we propose a framework, the unconscious binding hypothesis, to distinguish unconscious processing from conscious processing. According to this framework, the unconscious mind not only encodes individual features but also temporally binds distributed features to give rise to cortical representation, but unlike conscious binding, such unconscious binding is fragile. Under this framework, we review evidence from psychophysical and neuroimaging studies, which suggests that: (1) for invisible low level features, prolonged exposure to visual pattern and simple translational motion can alter the appearance of subsequent visible features (i.e. adaptation); for invisible high level features, although complex spiral motion cannot produce adaptation, nor can objects/words enhance subsequent processing of related stimuli (i.e. priming), images of tools can nevertheless activate the dorsal pathway; and (2) although invisible central cues cannot orient attention, invisible erotic pictures in the periphery can nevertheless guide attention, likely through emotional arousal; reciprocally, the processing of invisible information can be modulated by attention at perceptual and neural levels.

49 **Key Words:** Adaptation; Aftereffect; Afterimage; Amygdala; Attention; Awareness; Binocular
50 rivalry; Consciousness; Continuous flash suppression; Cortical pathways; Dorsal pathway;
51 Emotion; Magnocellular channel; Parvocellular channel; Priming; Subcortical pathways; V1;
52 Ventral pathway; Visual cortex

53

54 **Abbreviations:** AE, aftereffect; AI, afterimage; BR, binocular rivalry; CFS, continuous flash
55 suppression; FFA, fusiform face area; fMRI, functional magnetic resonance imaging; IT, monkey
56 inferotemporal cortex or inferior temporal cortex; LGN, lateral geniculate nucleus; LOC, lateral
57 occipital complex; M pathway, magnocellular pathway; MT, monkey medial temporal visual area;
58 MT+ (hMT+), human motion processing complex; P pathway, parvocellular pathway; SC,
59 superior colliculus; STS, superior temporal sulcus; V1 (2, 3, 4, 5, 7, and 8), visual cortical area1(2,
60 3, 4, 5, 7, and 8); V3A, V3 accessory

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70	Contents
71	1. Introduction
72	2. A theoretical framework
73	3. The scope and limits of unconscious processing during binocular rivalry
74	3.1. Feature analysis
75	3.2. Object and semantic processing
76	3.3. Face perception
77	3.4. Attentional guidance by invisible information
78	3.5. Attentional modulation of invisible information processing
79	4. Conclusions
80	Acknowledgements
81	References
82	
83	
84	
85	
86	
87	
88	
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90	

91 **1. Introduction**

92 In everyday life, our two eyes usually receive similar inputs from visual environment. What if
93 each of the two eyes views dissimilar images, as illustrated in Fig. 1? Rather than melding into
94 a stable composite, the two images rival for visibility, with one temporarily dominating
95 perception for seconds and being replaced in dominance by the other in turn (Fig. 1a). This
96 perceptual illusion is binocular rivalry (BR, for a review see Blake, 2001). According to Wade
97 (1998), BR was first reported by Porta in 1593, who viewed different pages from two books
98 with a partition between his two eyes.

99
100 **[insert figure 1 about here]**

101
102 Recently, there is growing interest in using BR to explore the dynamical properties of visual
103 awareness and its neural concomitants (for a review, see Tong *et al.*, 2006). The neural correlates
104 of consciousness are defined by Koch (2004, p. 16) as “the minimal set of neuronal events and
105 mechanisms jointly sufficient for a specific conscious percept”. Fundamental to this quest is to
106 understand the neural correlates of processing with and without awareness. In other words, if the
107 two experimental conditions differ only in awareness with sensory inputs kept constant, then the
108 neural differences between the two conditions should correlate with awareness. Unlike backward
109 masking or crowding, wherein awareness is manipulated by changing visual stimulation (e.g.
110 timing and spacing, respectively), in BR, visual stimulation is invariant yet the observer’s
111 conscious state is continually in flux (for a review of different psychophysical techniques for

112 manipulating visual awareness, see Kim and Blake, 2005). Moreover, some limitations of BR in
113 studying the neural correlates of awareness, such as unpredictable switches in perception and
114 relatively short suppression duration, can be surmounted by a recent technique derived from
115 rivalry—continuous flash suppression (CFS, Fang and He, 2005; Tsuchiya and Koch, 2005). In
116 CFS, a series of different, contour-rich, high-contrast patterns are continuously flashed to one
117 eye at about 10 Hz to suppress information presented to the other eye (Fig. 1b). CFS is effective
118 and reliable in suppressing even highly salient images throughout a relatively long viewing
119 period, sometimes longer than 3 minutes; as a comparison, visual masking renders visible
120 information invisible by presenting the stimuli less than 33 ms to establish objective
121 unawareness (**Box 1**). Such a long period of subliminal processing in CFS might produce robust
122 behavioral and neurophysiological effects, such as priming and subliminal conditioning. On the
123 other hand, CFS entails deeper suppression than BR does. For example, when measured with
124 gratings in a probe detection task, the contrast increment thresholds of CFS and BR (vs.
125 non-rivalry conditions) are 1.4 log-units and 0.5 log-units, respectively (Tsuchiya *et al.*, 2006).
126 For these reasons, CFS, albeit new, is now widely used to suppress visual stimuli from awareness
127 (Bahrami *et al.*, 2007; Fang and He, 2005; Gilroy and Blake, 2005; Jiang *et al.*, 2006; Jiang *et al.*,
128 2007; Jiang and He, 2006; Moradi *et al.*, 2005; Pasley *et al.*, 2004; Tsuchiya and Koch, 2005;
129 Yang *et al.*, 2007). The main finding is that weak signal that fails in the competition for
130 conscious representation can still produce significant behavioral effects and neural activations.
131
132 One of the central questions in interocular suppression (i.e. the suppression of an image from

133 awareness by BR or CFS) and consciousness in general, is the processing level of suppressed
134 information. In other words, *what is the fate of unconscious information and where does it*
135 *reach within the brain?* This is an essential question to consciousness because it constraints the
136 distinction between consciousness and unconsciousness. If unconscious information cannot be
137 processed at all regardless of how it is rendered invisible (i.e. it is as if no information is
138 presented), this would prove that consciousness and unconsciousness are profoundly different at
139 the earliest stage and easy to distinguish at both behavioral and neural levels. If, on the other
140 hand, unconscious information is processed to the same extent as conscious information in the
141 brain except for conscious state, this would imply that the only difference between
142 consciousness and unconsciousness is human subjective experiences. As one can imagine, the
143 real story is much more complicated than the two extremes: unconscious information can be
144 processed to some extent contingent on factors such as the types of stimuli and attentional
145 resources.

146
147 We propose that the brain not only can encode invisible features (orientation, motion direction,
148 etc.) but also can temporally bind distributed invisible features to give rise to cortical
149 representation, although such unconscious binding is fragile. In the sessions to follow, we will
150 first briefly review the scope and limits of unconscious processing during BR/CFS (see Kouider
151 and Dehaene, 2007 for a review on visual masking) to advocate our theoretical framework: the
152 unconscious binding hypothesis. Then we will discuss in details the depth of invisible
153 information processing for different types of information, ranging from features, objects, tools,

154 faces, to affective information. This will be followed by a discussion of the functional role
155 (especially attentional guidance) of invisible information, and how invisible processing can be
156 modulated by top-down attention. Finally, we will close the article with the take-home
157 messages from this area of research.

158

159 **[insert box 1 about here]**

160

161 **2. A theoretical framework**

162 Imagine that a triangle or a square is presented so briefly that you feel you are unable to see it,
163 yet if you are forced to choose one of the two, your accuracy in guessing the identity of the
164 image might nevertheless be significantly better than chance level. To probe the scope of
165 processing without awareness, we need to establish chance performance during such
166 forced-choice procedure. This might seem paradoxical: how can humans be affected by stimuli
167 that “absolutely” cannot be perceived? The central idea of perception without consciousness
168 lies in that *during the multiple stages of processing, consciousness emerges only after elaborate*
169 *perceptual processing* (Erdelyi, 1974). When the processing stages that give rise to
170 consciousness are interrupted, information is processed unconsciously to a certain degree
171 contingent on factors such as stimulus saliency and attentional capacity. Theoretically, the ideal
172 technique to characterize the depth of processing is to disrupt only the stage (s) prior to the
173 emergence of consciousness. It is unclear, however, exactly which stage (s) and what parts of
174 the brain that give rise to consciousness. A basic and fruitful approach is to probe the depth of

175 processing under unconscious state at both behavioral and neural levels. This is somewhat
176 similar to how attention researchers tackle the debate of early vs. late selection in attention (i.e.
177 whether attention exerts its modulation effect at an early sensory stage or at a late response
178 stage)—the crux is to understand the processing fate of unattended stimuli (Kanwisher and
179 Wojciulik, 2000; Lavie, 1995).

180

181 What can BR and CFS tell us in this sense? BR is effective in blocking information from
182 reaching awareness. Phenomenonally, observers are often unable to detect changes of a
183 suppressed target unless those changes are accompanied by abrupt transient changes in
184 luminance or contrast (Blake and Fox, 1974b; Blake *et al.*, 1998). To assess visual sensitivity
185 during suppression experimentally, Fox and colleagues developed the test-probe
186 procedure—probes (i.e. targets) are briefly presented to an eye during either dominance or
187 suppression phase to assess visual sensitivities to them (for a review, see Blake, 2001). They
188 found that suppression entails a general, non-selective loss in visual sensitivity of the
189 suppressed eye—probes presented in the suppressed eye are more difficult to detect than those
190 in the dominant eye (Wales and Fox, 1970), even when the probes differ significantly from the
191 original suppressed stimuli (Fox and Check, 1968; Fox and Check, 1972).

192

193 To evaluate what can be processed under suppression, besides the test-probe procedure,
194 researchers tap into several techniques including *adaptation* (**Box 2**) and *priming* (i.e. prior
195 experience increases sensitivity to subsequent related stimuli). To what extent can interocularly

196 suppressed information be processed? The results are mixed. After adaptation, some behavioral
197 aftereffects (AEs) (for an introduction to a variety of visual aftereffects, see **Box 3**), especially
198 low-level AEs (e.g. pattern and translational motion AEs), can be largely preserved during
199 interocular suppression under certain conditions; certain brain areas, particularly the amygdala
200 and dorsal cortical areas, exhibit robust activities for fearful faces and tools, respectively, as
201 measured by functional magnetic resonance imaging (fMRI). Other behavioral AEs and priming
202 effects, however, are severely disturbed, especially high-level AEs (e.g. complex motion and
203 face identity AEs), semantic priming, and cueing information. To explain the behavioral
204 findings, especially why simple features, but not complex features and objects, can be
205 processed, Blake (1997) proposed that 1) rivalry suppression disrupts the binding of local
206 features into coherent, global representations; 2) suppression transpires within visual areas
207 forming a pathway into the parietal lobe, several stages away from V1 (also known as primary
208 visual cortex, striate cortex, or Brodmann's area 17), where local features are registered. A
209 decade after this account was postulated, emerging studies especially those using fMRI have
210 cumulated; some findings, however, cannot fit into this proposal and wait for theoretical
211 understanding. For example, why behavioral studies fail to find object priming effect and face
212 adaptation whereas fMRI studies show neural activity to objects and fearful faces in dorsal
213 stream and the amygdala/ superior temporal sulcus (STS), respectively? This mirrors the
214 complication of the depth of unconscious processing in BR.

215
216 In this paper, we argue that both the conscious and unconscious minds face the binding problem

217 (Treisman, 1996): since different visual features are processed by functionally distinct neural
218 pathways and brain areas (Livingstone and Hubel, 1988; Felleman and Van Essen, 1991), how
219 does the brain subsequently match the correct features (e.g. a red bar moving rightward and a
220 green bar moving leftward) and how does it know which features belong to which objects (e.g.
221 a red apple as red, with a yellow banana as yellow but not the reverse)? It has been proposed
222 that solutions to the perceptual binding problem could take place at two different stages of
223 visual processing: an early and automatic binding based on spatiotemporal concurrence
224 (Holcombe and Cavanagh, 2001) and a late, object-based mechanism mediated by attention to
225 bind distributed features to correctly form coherent object representations (Treisman, 1999;
226 Wolfe and Cave, 1999). We propose here that binding during unconscious processing is
227 possible, albeit fragile: the brain can associate, group, or bind certain features in an invisible
228 scene to form certain cortical representation, and such binding can be detected under optimal
229 conditions. Although it remains to be determined in which circumstances can early binding and
230 late binding occur unconsciously, we speculate that early binding is automatic if attention is
231 paid and that late binding can occur if different features are strongly represented and attention is
232 sufficiently allocated to them (cf. Melcher and Vidnyanszky, 2006). Under this framework, we
233 review evidence from unconscious processing of low-level visual features (e.g. orientation,
234 spatial frequency), and then proceed to high level visual categories (e.g. objects, tools, and
235 faces), affective and attentive processing. In the following, the scope and limits of unconscious
236 processing in interocular suppression will be discussed and organized in five themes: 1) feature
237 analysis; 2) object (semantic) processing; 3) emotional processing; 4) attentional guidance by

238 invisible information; and 5) attentional modulation of invisible information processing.

239

240

[insert box 2 about here]

241

242 **3. The scope and limits of unconscious processing during binocular rivalry**

243 **3.1. Feature analysis**

244 To what extent are cortical areas (e.g. V1) supporting feature analysis spared during interocular
245 suppression and thus not directly involved in consciousness (Crick and Koch, 1995; Lin, 2008)?

246 At one extreme all basic features (orientation, spatial frequency, etc.) can be processed in
247 suppressed condition to the same extent as in dominant condition, and thus the cortical areas
248 supporting such feature analysis are not directly involved in consciousness (*all-exemption*
249 *hypothesis*). At the other extreme, no basic feature can be processed no matter what, and thus all
250 responsible cortical areas are involved in consciousness (*null-exemption hypothesis*). An
251 intermediate position is that when suppressed features can be processed but to a lesser extent
252 depending on the type of the features, and thus underlying cortical areas are involved in
253 consciousness (*partial-exemption hypothesis*). The critical test is to characterize the levels of
254 perceptual and neural processing across a range of features under suppressed and dominant
255 conditions.

256

257 The *null-exemption hypothesis* is unambiguously falsified by behavioral adaptation studies, as
258 summarized in Table 1. Early studies show that, under some conditions, interocular suppression

259 does not reduce the strengths of AEs after adaptation to a variety of low-level features
260 (definitions of AEs mentioned in the following are provided in **Box 3**): tilted lines (tilt AE,
261 Wade and Wenderoth, 1978), squarewave gratings (spatial frequency AE, including contrast
262 threshold elevation and spatial frequency shift, Blake and Fox, 1974a), McCollough-type
263 gratings (orientation-contingent color AE, White *et al.*, 1978), and translational motion (motion
264 AE, Lehmkuhle and Fox, 1975; O'Shea and Crassini, 1981). Is this evidence for the
265 *all-exemption hypothesis*, that the neural basis of these AEs, such as V1 and MT+, are not
266 directly related to visual awareness? The critical test to tease apart the *all-exemption hypothesis*
267 and the *partial-exemption hypothesis* is to clarify the relative strengths of AE after adaptation to
268 suppressed and dominant stimuli. Two recent studies provide behavioral evidence for the
269 *partial-exemption hypothesis*: the strength of negative AI after adaptation to suppressed (vs.
270 visible) oriented gratings was significantly weaker during BR (Gilroy and Blake, 2005) and
271 CFS (Tsuchiya and Koch, 2005). Moreover, monkey single-unit recordings (Leopold and
272 Logothetis, 1996; Sheinberg and Logothetis, 1997), human electroencephalogram recordings
273 (Cobb *et al.*, 1967; Lansing, 1964), and functional neuroimaging (Haynes *et al.*, 2005; Lee *et al.*,
274 2005; Lumer *et al.*, 1998; Polonsky *et al.*, 2000; Tong and Engel, 2001; Wunderlich *et al.*, 2005)
275 show robust awareness-dependent modulations in V1—neural events in V1 are attenuated in
276 response to suppressed (vs. dominant) visual stimuli. Thus, these studies demonstrate that V1 is
277 directly involved in visual awareness, supporting the *partial-exemption hypothesis* (Lin, 2008).
278 How to reconcile the discrepancy between the behavioral adaptation and neurophysiological
279 studies? Blake *et al.*, (2006) provided a nice resolution to this debate (Figure 2). This study taps

280 into the finding that some visual AEs depend critically on the contrast of the adaptor, with the
281 strength of adaptation saturating at moderate to high contrast levels (Figure 2a). Critically,
282 full-strength AEs observed in previous studies might only hold for high contrast adaptor. Indeed,
283 using high contrast adaptors, Blake et al., (2006) replicated previous studies; however, using
284 low contrast adaptors, they showed that interocular suppression did weaken the strength of
285 threshold elevation AE and motion AE (Figure 2c-d). This implies that at least some of the
286 neural events underlying rivalry suppression transpire before or at the site(s) of threshold
287 elevation and motion adaptation. Presumably, the neural mechanisms of threshold elevation and
288 motion AEs are closer than those of AEs that are not modulated by awareness to the neural
289 correlates of consciousness.

290
291 **[insert figure 2 about here]**

292
293 Further support for the partial-exemption hypothesis calls for evidence that some (presumably
294 complex) features might not be processed at all when suppressed. Motion AE (MAE) is an
295 excellent candidate for testing this idea because of its rich variety. As mentioned above,
296 translational (i.e. linear) MAE is largely spared during suppression, similar to the finding of
297 preserved motion priming after suppression (Blake *et al.*, 1999). Importantly, however,
298 Wiesenfelder and Blake (1990) did observe that the duration of spiral AE after adaptation to
299 spiral was proportional to the total duration of spiral visibility during adaptation, similar to the
300 disruption of the drifting plaid-induced MAE during suppression (van der Zwan *et al.*, 1993).

301 Further evidence comes from illusory AE: subjective (i.e. illusory) contour AE (van der Zwan
302 and Wenderoth, 1994) and square-wave illusion AE (Blake and Bravo, 1985), which are
303 believed to arise from intercortical interactions in early visual areas (e.g. V1 and V2, Lee and
304 Nguyen, 2001), are also disrupted during suppression. Thus, some complex features such as
305 spiral, drifting plaid, illusory contour, and square-wave illusion are almost completely disrupted
306 during interocular suppression.

307
308 The picture that emerges from these adaptation studies is that all visual features can be
309 modulated by visual awareness to different degrees. Processing of basic features (e.g. tilts and
310 simple motions) is modulated by visual awareness to a lesser extent than processing of complex
311 features (e.g. complex motions); when contrast of basic features is high, such processing can be
312 even exempted from modulation by consciousness. In neural terms, V1 feature analyzers, albeit
313 inhibited to a certain extent, are largely responsive to suppressed visual features compared with
314 later visual areas (such as MT+). This suggests that interocular suppression occurs at early
315 stages of processing and increases at later cortical stages, as elaborated in the following sections.
316 A more complete picture entails moving beyond feature analysis to examine the processing of
317 higher level visual inputs.

318

319 **[insert box 3 about here]**

320

321 **[insert table 1 about here]**

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323 **3.2. Object and semantic processing**

324 To what extent can objects and semantic information be processed unconsciously? Given that
325 complex features are deeply suppressed during BR (see 3.1. Feature analysis), it seems that
326 object representation and semantic analysis are almost impossible. Indeed, accumulating
327 evidence suggests 1) that the face identity-specific AE observed in visible condition is
328 effectively cancelled by interocular suppression (Moradi *et al.*, 2005), 2) that pictorial object
329 priming in a naming task can be found only for stimuli that are processed sufficiently to be
330 identified in the priming stage (Cave *et al.*, 1998), and 3) that word-priming effect in a
331 word/non-word decision task can be measurable only if the observers consciously perceive the
332 prime words (Zimba and Blake, 1983). These observations raise an intriguing question
333 regarding the neural basis of the disruption of object processing and semantic priming during
334 suppression. According to Lamme and Roelfsema (2000), it seems that encoding of simple
335 features (e.g., spatial frequency) is hardwired and occurs without awareness when information
336 first enters early visual cortex in a feedforward sweep. These features are then attentively
337 grouped to enter consciousness through recurrent processing, by means of horizontal
338 connections and feedforward/feedback projections. Built on this, there are two possible
339 accounts for the disruption of object processing and semantic priming: one account suggests
340 that all basic visual features of objects are processed to some extent, with the disruption due to
341 inefficient attentive grouping or recurrent processing (i.e. *grouping disruption account*); the
342 other account, which we favors, maintains that some critical features of objects are disrupted,

343 such that binding/grouping is impossible simply because of missing critical features, in
344 conjunction with potential grouping inefficiency (i.e. *feature disruption account*). The latter
345 account is consistent with our unconscious binding framework; binding is possible during
346 unconscious processing if critical features can be registered and attentively grouped. To date,
347 there is no convincing evidence regarding this issue. Below, we discuss some recent advances
348 regarding the neural representation of object and semantic information during suppression. Note
349 that this approach is descriptive rather than explanatory because it cannot falsify either the
350 grouping disruption account or the feature disruption account.

351
352 The current state-of-the-art regarding the mechanisms of BR is that interocular suppression *per*
353 *se* occurs at early stages of processing (e.g. the lateral geniculate nucleus (LGN), Haynes *et al.*,
354 2005; V1, Polonsky *et al.*, 2000) and increases at subsequent cortical stages in both the ventral
355 (form) and the dorsal (motion) pathways, possibly due to cumulative lateral competition
356 (Nguyen *et al.*, 2003). In particular, neural activity within object-selective areas in the ventral
357 pathway, especially the inferotemporal cortex (IT)¹, is almost completely suppressed (Sheinberg
358 and Logothetis, 1997; Tong *et al.*, 1998). The IT plays an important role in both object
359 recognition and semantic processing. First, the IT is critical for object recognition in non-human
360 primates and humans. In primates, the IT codes complex objects and is responsible for view-

¹ The inferotemporal cortex (IT) is composed of the middle temporal gyrus and inferior temporal gyrus in humans. Although the inferior temporal cortex may indicate the ventral part of the inferotemporal cortex in humans, most people do not care about this point, and both terms are used interchangeably (K. Tanaka, personal communication, November 26, 2007).

361 and position-invariant object representations (Tanaka, 1996; Ungerleider and Mishkin, 1982). In
362 humans, the IT, which comprises the ventral surface of the human brain, extending from around
363 the occipito-temporal border to the middle part of the temporal cortex (Tanaka, 1997), is also
364 vital for object perception, as demonstrated by numerous studies such as those using fMRI
365 adaptation—the observation of decreased neural activity for repeated versus novel stimuli
366 (Grill-Spector *et al.*, 2006; for an overview, see Box 2). For example, repetition priming for
367 objects is observed in mid-levels of the neural processing hierarchy, including extrastriate
368 visual cortex extending into the IT and left dorsal prefrontal cortex, but not early visual areas or
369 motor areas (Buckner *et al.*, 1998). The disruption of object priming effect during BR, therefore,
370 might be due to the suppression of the ventral pathway, where the human homologue of the
371 monkey IT is located. Second, the IT also plays an important role in semantic processing: the
372 semantic neural network extends from left inferior frontal cortex into the IT lobe, and includes
373 occipital cortex and the fusiform gyrus (Tyler *et al.*, 2001). Although with backward masking
374 several studies have observed object recognition priming, or word priming, or both (Dehaene *et*
375 *al.*, 2001; Dehaene *et al.*, 2004; Dell'Acqua and Grainger, 1999; Devlin *et al.*, 2004; Gaillard *et*
376 *al.*, 2006; Kiefer and Brendel, 2006; Naccache *et al.*, 2005; Nakamura *et al.*, 2005), these
377 findings are probably due to incomplete disruption of the IT. For example, IT neurons in the
378 macaque monkeys retain substantial information about the target images despite visual masking
379 (Rolls *et al.*, 1999).

380

381 Although the proposal that interocular suppression deepens in later stages (Nguyen et al. 2003)
382 receives large amounts of evidence in the ventral pathway as reviewed above, it is not clear
383 whether the same holds for the dorsal pathway. In particular, the functional organization of the
384 visual pathways in the cerebral cortex comprises not only the ventral “vision-for-perception” (i.e.
385 to obtain information about the features of objects) pathway but also the dorsal “vision-for-action”
386 (i.e. to guide movements) pathway (Goodale and Milner, 1992). The ventral and dorsal pathways
387 carry out different computations on visual information from the retina: the former recognizes an
388 object independent of its size, momentary orientation, and position; the latter computes the
389 absolute metrics of target objects in a frame of reference centered on specific effectors (i.e.
390 egocentric coding). Failing to observe object/semantic priming effect and the disruption of
391 ventral visual areas (e.g. the IT) during suppression, therefore, need not be interpreted that
392 objects or words cannot be processed at all. In particular, although areas such as the lateral
393 occipital complex (LOC) in the ventral pathway show preferential activation to images of objects
394 (Malach *et al.*, 1995), the dorsal pathway also has several object-sensitive areas, including
395 V3A/V7 (Grill-Spector et al., 1998) and intraparietal sulcus (Grill-Spector et al., 2000).
396 Importantly, the object-sensitive regions in the dorsal pathway differ from those in the ventral
397 pathway—the dorsal object areas, presumably because of its important role in reaching and
398 grasping, prefer manipulable objects such as man-made tools, which are commonly associated
399 with specific hand movements (Chao and Martin, 2000). Thus tools are a unique category of
400 objects and serve as an excellent candidate to test the level of object processing in the dorsal
401 pathway. Using fMRI, Fang and He (2005) showed that dorsal cortical areas (including V3A, V7,

402 and part of the intraparietal areas) responded strongly to different types of visual objects
403 suppressed by CFS, with stronger responses to images of tools than human faces (Figure 3). This
404 study provides evidence that suppressed invisible images of tools can activate the dorsal pathway
405 and fits nicely with the perception–action model (Goodale and Milner, 1992). The action
406 interpretation is further reinforced by the observation that when the motion of a rival stimulus is
407 consistent with self-generated actions during BR, such actions can extend the dominance
408 durations and abbreviate the suppression durations of that stimulus (Maruya *et al.*, 2007).

409

410

[insert figure 3 about here]

411

412 How to reconcile the discrepancy between ventral and dorsal activity to invisible objects? That
413 ventral activity is almost abolished whereas dorsal activity is somehow preserved in interocular
414 suppression might reflect the functional differences between the parvocellular (P) and
415 magnocellular (M) channels, in terms of selectivity to spatial and temporal frequency, color,
416 motion, and luminance contrast (Box 4). The P and M pathways are preferentially associated
417 the ventral and dorsal cortical pathways, respectively. Such distinctions between the P and M
418 pathways potentially form part of the anatomical basis of different sensitivity of interocular
419 suppression in the ventral and dorsal pathways. It is proposed that rivalry transpires mainly in
420 the P pathway with visual information in the M pathway escaping rivalry suppression (Carlson
421 and He, 2000; He *et al.*, 2005). Building on this *sensitivity account*, Fang and He (2005)
422 suggested that the dorsal activation to images of tools might arise from the residual signal after

423 incomplete suppression in visual cortex or from subcortical projections. At least two important
424 issues, however, remain unclear. The first issue concerns the functional significance of such
425 dorsal activity for tools: what are the behavioral consequences and why? One approach to
426 address this issue is to characterize the levels of representation for tools, using adaptation and
427 priming methods. The second issue involves the neurophysiological origins of dorsal activity
428 for invisible tool images: does tool information get to the dorsal pathway through V1, or
429 subcortical projections, or both? Neither the grouping disruption account (i.e. suppression
430 disrupts grouping of simple features of objects) nor the feature disruption account (i.e.
431 suppression disrupts processing of critical features of objects) could disambiguate the
432 subcortical vs. cortical origins, nor could the sensitivity account of P and M. It seems that such
433 ambiguity of neurophysiological origins is a general issue in neuroscience and might reflect the
434 complicated connections in the nervous system. For example, area MT receives not only inputs
435 from V1, V2, and V3 (DeYoe and Van Essen, 1988), but also direct projection from the LGN in
436 the macaque monkeys (Sincich *et al.*, 2004). To distinguish subcortical and cortical
437 contributions, several important questions warrant empirical investigations. First, if rivalry
438 indeed transpires mainly in the P pathway but not the M pathway, then why? It's unclear how P
439 and M cells differ in this aspect, and how the cells within each pathway differ from each other.
440 Given that the ventral pathway receives inputs from both P and M cells (Merigan and Maunsell,
441 1993), it is reasonable to speculate, based on the P and M sensitivity account, that there should
442 be some activity in the ventral pathway from M cells during interocular suppression. Second,
443 how to isolate the interconnections between different areas in the brain? Such interconnection

444 makes it difficult to distinguish subcortical vs. cortical contributions as it is almost impossible
445 to isolate subcortical contributions or cortical contributions from V1 for cortical activity in the
446 dorsal pathway. Current neuropsychology research sheds little light on this issue. For instance,
447 although blindsight patients with a lesion in V1 can display preserved visually based action, this
448 is not direct evidence that subcortical pathways are sufficient for dorsal activity to invisible
449 images of tools in the Fang and He study; it is just unlikely that V1 is totally damaged in these
450 patients. Monkey lesions studies will help to resolve this issue. In humans, a possible approach
451 might be to examine attentional modulation of dorsal activity to tools, and to elucidate and
452 quantify the differences in attentional modulation of subcortical and cortical pathways (see 3.3.
453 Face perception).

454
455 In summary, behaviorally, object identification and semantic analysis are largely depleted during
456 interocular suppression. Neural activity in the ventral pathway is almost completely disrupted;
457 however, there is still considerable amount of activity in the dorsal pathway to images of some
458 categories of objects, such as tools, which provides neural evidence for the neuropsychological
459 observation of action without identification. That invisible images of tools can activate the dorsal
460 pathway supports our unconscious binding hypothesis in that at least it suggests that certain
461 features are bound to give rise to dorsal object-sensitive areas.

462
463 **[insert box 4 about here]**

464

465 **3.3. Face perception**

466 As a special category of objects, the face is processed differently from other categories of
467 objects (Farah *et al.*, 1998) with dedicated neural substrates (e.g. the fusiform face area, FFA,
468 Kanwisher *et al.*, 1997; the occipital face area, OFA, Halgren *et al.*, 1999). Although activity in
469 the FFA for suppressed faces is almost entirely abolished (Fang and He, 2005; Pasley *et al.*,
470 2004; Tong *et al.*, 1998; but see Jiang and He, 2006), invisible fearful faces can robustly
471 activate the left amygdala (Jiang and He, 2006; Pasley *et al.*, 2004; Williams *et al.*, 2004) and
472 the STS (Jiang and He, 2006). For instance, using CFS, Jiang and He (2006) observed that
473 visibility did not modulate activity for *fearful* faces but had a profound effect for *neutral* faces
474 in the amygdala. Similarly, in the STS, activity was robust to invisible *fearful* faces but not to
475 *neutral* faces. On the contrary, in the FFA, activity was still measurable, albeit much reduced, to
476 both *fearful* and *neutral* faces.

477
478 Reminiscent of the unclear origins of the dorsal activity for tools (see 3.2. Object and semantic
479 processing) is the debate regarding whether activity in the amygdala to invisible fearful faces is
480 due to projections from cortical or subcortical pathways. Accumulating evidence from both
481 experimental animals and humans seems to favor the subcortical account. Rodents, for example,
482 exhibit fear conditioning with auditory or visual stimuli without respective sensory cortex
483 (Armony *et al.*, 1997; Romanski and LeDoux, 1992). Similarly, blindsight patients with a lesion
484 in V1 nevertheless exhibit residual abilities to detect and localize visual stimuli (Weiskrantz,
485 1997) and recognize facial expressions (de Gelder *et al.*, 1999); engagement in the latter task

486 activates the amygdala (Morris *et al.*, 2001). Convergent evidence comes from healthy humans.
487 For example, Morris et al. (1999) measured neural activity for two angry faces, one of which
488 was associated with a burst of white noise through previous classical conditioning. When
489 rendered invisible by backward masking with a neutral face, the conditioned angry face
490 (compared with the unconditioned angry face) enjoyed increased connectivity among the *right*
491 amygdala, the pulvinar, and the SC but decreased connectivity among the *right* amygdala, the
492 fusiform, and the orbitofrontal cortex. When the conditioned angry face was visible, however,
493 such co-variation disappeared. On the other hand, the *left* amygdala could not differentiate
494 aware and unaware conditioned angry faces; its connectivity with the pulvinar and the SC
495 showed no context-specific co-variation. These data suggest a subcortical pathway that enables
496 invisible stimuli to access the amygdala. A further demonstration of subcortical but not cortical
497 pathways' involvement in invisible fearful face processing is provided by Pasley and colleagues
498 (2004). They found that, invisible fearful faces (compared with non-face objects) activated the
499 amygdala but not the IT, which suggests that rudimentary discrimination of certain complex
500 visual patterns does not require a high-level cortical representation.

501
502 However, competing evidence argues otherwise. For instance, anatomically the crucial link
503 between the pulvinar and the amygdala has not been demonstrated in primates yet (Pessoa,
504 2005). In addition, results from blindsight patients are ambiguous because in the same
505 blindsight patients invisible information can also activate cortical areas. This alternative
506 explanation renders it impossible to rule out the contribution of cortical pathways (e.g.

507 extrastriate areas) in processing fearful faces. For example, images of complex objects
508 presented in the blind visual field activate several visual areas, including MT+/V5 to rotating
509 spiral stimulus, and lateral occipital cortex (MT+/V5 and the LOC) and posterior fusiform
510 gyrus (V4/V8) to coloured images of natural objects (Goebel *et al.*, 2001). It is therefore
511 desirable to see whether invisible fearful faces can activate the amygdala in blindsight patients
512 with full lesions in visual pathways.

513
514 How to tease the two accounts apart then? To tackle the cortical-subcortical debate, one
515 approach is to use features that can distinguish cortical from subcortical processing. First,
516 although anatomically both cortical and subcortical pathways terminate at the amygdala, they
517 come with different transmission properties (Pessoa, 2005). For instance, in primates the IT
518 (Nakamura *et al.*, 1992; Stefanacci and Amaral, 2002), but not earlier visual cortical areas (Iwai
519 and Yukie, 1987; Webster *et al.*, 1991), slowly passes detailed information to the amygdala. On
520 the contrary, information transmission in the retinotectal pathway (i.e. the
521 retino-collicular-pulvinar-amygdala pathway, an important subcortical pathway which proceeds
522 from the retina to the SC, posterior nuclei of the thalamus such as the pulvinar, and then onto
523 the amygdala) is rapid and shallow (LeDoux, 2000). Critical to the current reasoning, this
524 means that subcortical pathways are able to (relatively) surpass attentional modulation
525 (Anderson *et al.*, 2003; Vuilleumier *et al.*, 2001) and visibility constraint (Morris *et al.*, 1998;
526 Whalen *et al.*, 1998), but unable to analyze visual inputs in a fine-grained scale (Anderson *et al.*,
527 2003; Williams *et al.*, 2004). It is observed, for example, that activity in the amygdala increased

528 significantly for happy versus neutral faces only when the faces were invisible (Williams *et al.*,
529 2004). Williams *et al.* argue that although the amygdala still encodes affective information from
530 the face stimuli, it has a limited capacity to differentiate affective valence when it must rely on
531 information from subcortical inputs. Second, spatial frequency is another feature that can
532 potentially distinguish the cortical and subcortical projections (for a review, see Johnson, 2005).
533 Specifically, the fusiform cortex favors *high spatial frequency* over low frequency face
534 regardless of emotional expressions, whereas the amygdala favors *low frequency* over high
535 frequency fearful faces. Evidence for the subcortical account comes from the observation that,
536 critically, low frequency but not high frequency fearful faces could activate the pulvinar and the
537 SC (Vuilleumier *et al.*, 2003). Third, a controversial one is whether the susceptibility to
538 attentional modulation may provide another tool to distinguish subcortical from cortical
539 processing. Pessoa and colleagues forcefully argue that a strongly automatic process should be
540 largely independent of attention, among other top-down factors including task context,
541 interpretation, and visual awareness (Pessoa, 2005). Indeed, using fMRI Pessoa and colleagues
542 (Pessoa *et al.*, 2002a; Pessoa *et al.*, 2002b) found that, if the task was sufficiently demanding,
543 activity in the amygdala and other areas was modulated by attention even for visible emotional
544 faces. When participants were totally unaware of the fearful faces that flashed for 33 ms, no
545 differential activation was observed in the amygdala (Pessoa *et al.*, 2006). Event-related
546 potentials (ERP) studies provide complementary evidence for this attentional modulation
547 argument. For example, a greater frontal positivity in response to arrays containing fearful faces,
548 relative to neutral faces, was obtained about 100 ms after stimulus onset only under attended

549 condition (Eimer *et al.*, 2003; Holmes *et al.*, 2003). Pessoa and colleagues reason that, given the
550 rich details contained in facial expressions, the critical pathway involved in processing
551 emotional expressions is cortical, which starts from V1 to extrastriate cortex, the fusiform, the
552 STS, the IT, and then to the amygdala. On the other hand, subcortical routes are insufficient to
553 give rise to activity in the amygdala to invisible emotional faces. Thus, they argue for the
554 cortical account.

555
556 Although there is no consensus regarding which pathways are more responsible for processing
557 invisible emotional expressions, we believe that accumulating evidence favors the subcortical
558 account. In particular, before those studies showing attentional modulation of invisible emotional
559 face processing can be taken as evidence against the subcortical argument, the assumption that a
560 truly subcortical pathway should be automatic and free of attentional modulation needs to be
561 grounded firmly. To us, this assumption has not been well supported. For example, although
562 relative to cortical pathways, subcortical pathways are less susceptible to attentional modulation,
563 they are still susceptible to attentional modulation (Kastner and Pinsk, 2004). Attention is
564 regarded as the gatekeeper of sensory inputs: in vision, attention modulates neural activity as
565 early as in the LGN (Chen *et al.*, 1998; O'Connor *et al.*, 2002) and the pulvinar (Kastner *et al.*,
566 2004; Robinson and Petersen, 1992); in audition, it starts as early as 20 ms after stimulus onset in
567 auditory cortex (Woldorff *et al.*, 1993). As such, attentional modulation should not be taken as
568 evidence against the involvement of subcortical pathways in invisible emotion processing. More
569 research is needed, though, to quantify attentional modulation of subcortical and cortical

570 processing. Moreover, the subcortical retinotectal pathway should be anatomically established in
571 primates. It is likely that the relative contributions from cortical and subcortical routes are
572 quantitative rather than mutually exclusive.

573

574 In conclusion, interocular suppression disrupts ventral temporal activity for faces, but not
575 amygdala activity for fearful faces. It is still a matter of debate, however, regarding the relative
576 contributions of subcortical and cortical projections to amygdala activity for invisible fearful
577 faces. Overall, accumulating evidence seems to favor the subcortical account, but more research
578 is needed to quantify the relative contributions of the two pathways, and to elucidate whether
579 subcortical inputs can be sufficient in processing invisible fearful faces. We speculate that
580 unconscious detection of fearful expression might result from binding of critical features (e.g.
581 mouth shape and eye shape), regardless of whether these critical features are conveyed through
582 subcortical or cortical pathways, or both.

583

584 **3.4. Attentional guidance by invisible information**

585 As elaborated above, information kept out of consciousness can nevertheless enter into the
586 brain and be processed at multiple stages, which raises an intriguing question about the
587 functional and ecological significance of unconscious processing. For example, can
588 unconscious information guide conscious processing? An important faculty of conscious
589 processing is attention, the ability to focus on a small portion of behaviorally relevant
590 information while filter out distracting information. Attention is fundamental to subsequent

591 processing, acting as an information-processing bottleneck, because at any single moment, our
592 environment bombards us with far more information than can be consciously registered and
593 effectively processed. It is thus intriguing to ask whether information suppressed during
594 BR/CFS can influence allocation of visual attention.

595

596 To address this, brain machinery in processing invisible information should be linked to its
597 potential role in deploying attention. At neural level, although there is no evidence that invisible
598 information can activate the frontoparietal network, which is important for controlling attention
599 (for an overview of the neural mechanisms of top-down and bottom-up control of attention, see
600 **Box 5**), there is evidence that invisible information can activate dorsal areas such as V3A, V7,
601 and part of the intraparietal areas (Fang & He, 2005). Behaviorally, the possibility of attentional
602 guidance by invisible information was first examined by Schall and colleagues (1993). In their
603 study, a black dot was used as an orienting cue, which appeared on either the left or right side of
604 the *central small circle*, signifying that the target would appear on either the left or right side of
605 the *screen*, respectively. The cue was either 80% or 90% valid (i.e. accuracy in predicting the
606 target location) and was presented during either the dominant (i.e. visible) or suppressed (i.e.
607 invisible) phase of BR. They found that reaction times to the targets were significantly affected
608 by cue validity only during the dominant phase but not during the suppressed phase. This
609 implies that symbolic central cues, when rendered invisible, cannot direct top-down attention. It
610 is unclear, however, whether this negative finding is due to ineffective guidance of attention (i.e.
611 the cue is processed but not to the degree of serving as an effective cue), or due to ineffective

612 cue processing (i.e. the cue is not processed at all). If the latter account is correct, then the null
613 attentional effect can be attributed to sensory analysis rather than attentional guidance *per se*.
614 More studies are needed to clarify this issue, the critical test being specifying the processing
615 levels of the cueing information.

616

617 Since attention includes not only top-down attention, which was explored by Schall and
618 colleagues (1993), but also bottom-up attention, it remains important to ask whether invisible
619 information can “capture” attention in a bottom-up manner. At the cortical level, it is unclear
620 whether suppressed information can activate the right ventral frontoparietal network, a critical
621 network for bottom-up attention (**Box 5**). At the subcortical level, although it is also unclear
622 whether the SC or the pulvinar are employed during suppression, there is some evidence that
623 the amygdala, which is responsive to invisible fearful faces, is able to guide attention. For
624 example, in the attentional blink (Raymond *et al.*, 1992), when several stimuli are briefly
625 displayed in sequence (i.e. rapid serial visual presentation), observers usually fail to detect a
626 second target when it is presented 200-500ms after the first one; importantly, compared with
627 normal stimuli, negative stimuli usually show a preferential ability to break through into
628 awareness. In support of the current reasoning, it has been shown that the amygdala is
629 important for such attenuation of the attentional blink. For example, when exposed to aversive
630 words, patients with left anterior–medial temporal lesions or bilateral amygdala lesions failed to
631 show attenuation of the attentional blink (Anderson and Phelps, 2001), implying a causal role of
632 the amygdala or the anterior-medial temporal cortex in enhancing emotion-related information

633 processing. The amygdala's ability to modulate the attentional blink may derive from its
634 reception of the rapid and crude information from the pulvinar in the thalamus through the
635 retinotectal pathway (Zald, 2003; see also 3.3 Face perception). Since suppressed fearful faces
636 can activate the amygdala, it seems logical to speculate that some invisible emotional
637 information might be able to attract attention automatically. Indeed, using invisible erotic
638 pictures, a recent study by Jiang et al. (2006) lends support to this hypothesis. As illustrated in
639 Figure 4, they presented participants with an erotic picture and a scrambled picture, both
640 rendered invisible by CFS, next to the central fixation point, one on each side. To assess
641 whether the invisible erotic picture could guide attention, they asked participants to indicate the
642 perceived orientation (clockwise or counterclockwise) of a briefly presented Gabor patch
643 following the presentation of the suppressed erotic images, which could be on the left or on the
644 right (Figure 4a). The logic is, if the erotic picture can automatically capture attention, then
645 participants should perform better when the Gabor patch is presented on the same (vs. different)
646 side as the erotic picture. The difference between the two conditions can be used to index the
647 amount of automatic attentional guidance (i.e. the implicit attentional effect). In other words, a
648 positive attentional effect means that attention is attracted to the erotic picture, whereas a
649 negative attentional effect means that attention is repelled from the erotic picture. Interestingly,
650 they found that invisible erotic pictures could either attract or repel observers' spatial attention
651 depending on their gender and sexual orientation. Specifically, for heterosexual participants,
652 attention was attracted to invisible erotic pictures of the opposite gender (and for males,
653 attention was repelled from invisible erotic pictures of the same gender; Figure 4b). Gay males

654 were similar to heterosexual female participants in that they were attracted to male erotic
655 pictures but not female erotic pictures. Bisexual females fell in-between the heterosexual male
656 group and the heterosexual female group. This study thus reveals the power of invisible
657 information in orienting attention, which is consistent with earlier studies including those
658 showing 1) that exogenous cues rendered invisible by visual masking can capture attention
659 (McCormick, 1997), and 2) that oriented Gabor patches, with such high spatial frequency that it
660 is perceptually indistinguishable from a uniform field, can generate orientation-dependent
661 spatial cueing effect (Rajimehr, 2004). It remains unclear what kind of information in the erotic
662 pictures is responsible for orienting attention. According to the unconscious binding hypothesis,
663 one possibility is that nude bodies in the erotic pictures, albeit invisible, increase arousal levels
664 of the observers through feature binding. Future research is needed to specify the conditions
665 that can generate top-down and bottom-up attention, and to reveal the neural mechanisms that
666 support such implicit attentional guidance.

667
668 **[insert figure 4 about here]**

669
670 In short, although invisible dot cues fail to provide cueing effect, invisible erotic images can
671 attract attention and boost performance in the locations where these images appear. Together
672 with other studies using masking to show orienting of attention, these results provide evidence
673 for the existence of implicit attention. According to the unconscious binding hypothesis, it is
674 likely that binding of certain critical features in the invisible erotic images generates

675 representation of arousal value. How the brain binds these critical features and the exact
676 mechanisms of attentional guidance by implicit information await future research.

677

678 **[insert box 5 about here]**

679

680 **3.5. Attentional modulation of invisible information processing**

681 It is now clear that information rendered invisible by BR or CFS can be processed to several
682 levels and functionally can guide attention. But what are the limits of such unconscious
683 processing? In particular, is invisible information processing constrained by concurrent
684 processing resources, or instead it is so automatic that it is not under the control of attention?

685

686 There is no unified view regarding the relationship between attention and awareness. On the
687 one hand, since both attention and awareness are selective in nature due to limited resources,
688 some argue that they are identical (O'Regan and Noe, 2001; Posner, 1994). On the other hand,
689 since we are able to attend to the locations of invisible images and can also become conscious
690 of the gist of a scene in the near absence of attention, others maintain that attention and
691 awareness can be dissociated (Koch and Tsuchiya, 2007; Lamme, 2003). To resolve this debate,
692 it is necessary to address some conceptual issues. First, is attention necessary for awareness? At
693 first glance this seems true (Dehaene *et al.*, 2006): we become aware of what the paper is
694 talking about only if we pay attention to it. To falsify this, we need to search for “awareness
695 without attention”; the critical test is whether we can perceive an image without attention. This

696 is partly supported by a study showing that we can be aware of the gist of a scene almost
697 without attention (Li *et al.*, 2002). Second, is attention sufficient for awareness? It is obvious
698 that attention is insufficient for awareness: we can attend to the locations of invisible
699 information but still be unaware of it, as in CFS. Thus, it seems that attention is neither
700 necessary nor sufficient for awareness.

701

702 The dissociable relationship between attention and awareness provides conceptual grounds to
703 ask how attention can modulate both aware and unaware visual processing. In aware condition,
704 attention plays a critical role in determining the quality of representation of incoming
705 information. On philosophical grounds, Block (2005) argues that awareness without attention is
706 short-lived and vulnerable (“phenomenal awareness”), analogical to retinotopic fleeting
707 memory (i.e. iconic memory for briefly presented visual stimuli); only with attention can
708 awareness become stable and deep (“access awareness”), analogical to durable non-retinotopic
709 memory (e.g. working memory). In neurobiological terms, when feedforward processing occurs
710 among early visual areas, phenomenal awareness arises; only when recurrent interactions grow
711 to include executive or mnemonic space (frontal, prefrontal, and temporal cortex) can access
712 awareness take place (Lamme, 2003). In other words, recurrent interactions between higher
713 brain areas and visual areas are necessary for awareness, with attention playing a critical role.

714

715 In unaware condition, does attention still play a critical role in determining how much we can
716 process? In other words, can invisible information processing be modulated by attention? The

717 critical test is to contrast invisible information processing under attended and unattended
718 conditions (for a discussion of the distinction between unattended stimuli and irrelevant stimuli,
719 see **Box 6**). A recent study with CFS (Kanai *et al.*, 2006) suggests that spatial attention could
720 not modulate the strength of the tilt AE induced by invisible adaptors, whereas feature-based
721 attention could. However, because they manipulated spatial attention by instructing the
722 observers to attend to one of the two spatial markers drawn on top of the Mondrian patterns,
723 this may not be effective in optimizing unattended condition—attention in one spatial marker
724 can still spill over to the other maker (Lavie, 1995; see also Box 6). Indeed, a recent study
725 (Bahrami *et al.*, 2007) made attentional load of the central task very high to deplete attentional
726 resource available in each trial, such that little attention would spill over to the task-irrelevant
727 distractors. Using such demanding task to load attention, they show that attention in the foveal
728 task strongly modulated retinotopic activity in V1 evoked by invisible objects. However, in the
729 same study attention failed to modulate V1 activity for noise stimuli used for CFS, making it
730 difficult to interpret the positive results of attentional modulation of invisible objects. It thus
731 remains unclear why attention fails to modulate neural activation for noise but succeeds in
732 modulating neural activity of invisible objects. Future research should address whether and how
733 attention dynamically modulates invisible information. For example, in the visual cortex,
734 attentional modulation of visible stimuli increases from early to late processing stages, but
735 attention effect in the LGN is larger than that in V1 (Kastner and Pinsky, 2004). Whether this
736 holds for invisible stimuli awaits empirical investigation. Interestingly, Bahrami *et al.* (2007)
737 show that attentional modulation effect was larger in V1 than V2 or V3. The time is ripe for

738 further investigations.

739

740 It thus appears that explicit attention can modulate invisible information processing. Several
741 questions remain open though. In particular, it is unclear whether, and how, different cortical
742 areas differ in sensitivity to attentional modulation during suppression. In addition, it is not
743 known how different types of attention, such as space-based attention (i.e. attention to locations)
744 and feature-based attention (i.e. attention to features), might show different modulation
745 properties. We suspect that attention is necessary to unconscious binding; moreover, without
746 attention, unconscious processing of features is not possible.

747

748 **[insert box 6 here]**

749

750 **4. Conclusions**

751 Human mental life extends well beyond conscious experiences. Although much has been
752 learned about BR, the mechanism of information processing during suppression remains elusive.
753 To understand this mechanism, we must understand the depth of information processing during
754 suppression at behavioral, neural, and theoretical levels. In this paper, we have advocated the
755 unconscious binding hypothesis, that binding of invisible features are possible albeit susceptible
756 to interference. Although this hypothesis is still in its infancy, the studies reviewed here provide
757 important insights. First, low level features can be processed unconsciously with processing
758 level modulated by awareness and attention. Second, high level representations of objects and

759 faces in the ventral visual areas are dramatically suppressed, but tools and emotional faces can
760 still activate dorsal areas and the amygdale, respectively. Third, invisible information can serve
761 as an implicit cue to guide attention, which we refer to “implicit attention”. Last, invisible
762 information in turn can be modulated by external explicit attention. Understanding the
763 mechanisms subserving invisible information processing will bring new insights into how the
764 visual system operates without consciousness, as well as the neural correlates of consciousness
765 in general.

766

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780 **References**

- 781 Addams, R. (1834) An account of a peculiar optical phenomenon seen after having looked at a
782 moving body, etc. *Lond. Edinb. Phil. Mag. J. Sci.* **5**, 373-374.
- 783 Amaral, D. G., Price, J. L., Pitkänen, A. and Carmichael, S. T. (1992) Anatomical organization
784 of the primate amygdaloid complex. In: *The Amygdala: Neurobiological Aspects of*
785 *Emotion, Memory, and Mental Dysfunction*. pp. 1–66. Ed. J. P. Aggleton. Wiley-Liss:
786 New York.
- 787 Anderson, A. K., Christoff, K., Panitz, D., De Rosa, E. and Gabrieli, J. D. (2003) Neural
788 correlates of the automatic processing of threat facial signals. *J. Neurosci.* **23**,
789 5627-5633.
- 790 Anderson, A. K. and Phelps, E. A. (2001) Lesions of the human amygdala impair enhanced
791 perception of emotionally salient events. *Nature* **411**, 305-309.
- 792 Armony, J. L., Servan-Schreiber, D., Romanski, L. M., Cohen, J. D. and LeDoux, J. E. (1997)
793 Stimulus generalization of fear responses: effects of auditory cortex lesions in a
794 computational model and in rats. *Cereb. Cortex* **7**, 157-165.
- 795 Aston-Jones, G., Rajkowski, J. and Cohen, J. (1999) Role of locus coeruleus in attention and
796 behavioral flexibility. *Biol. Psychiatry* **46**, 1309-1320.
- 797 Bahrami, B., Lavie, N. and Rees, G. (2007) Attentional load modulates responses of human
798 primary visual cortex to invisible stimuli. *Curr. Biol.* **17**, 509-513.
- 799 Blake, R. (1997) What can be "perceived" in the absence of visual awareness? *Curr. Dir.*
800 *Psychol. Sci.* **6**, 157-162.

- 801 Blake, R. (2001) A primer on binocular rivalry, including current controversies. *Brain & Mind* **2**,
802 5-38.
- 803 Blake, R., Ahlstrom, U. and Alais, D. (1999) Perceptual priming by invisible motion. *Psychol.*
804 *Sci.* **10**, 145-150.
- 805 Blake, R. and Bravo, M. (1985) Binocular rivalry suppression interferes with phase adaptation.
806 *Percept. Psychophys.* **38**, 277-280.
- 807 Blake, R. and Fox, R. (1974a) Adaptation to invisible gratings and the site of binocular rivalry
808 suppression. *Nature* **249**, 488-490.
- 809 Blake, R. and Fox, R. (1974b) Binocular rivalry suppression: insensitive to spatial frequency
810 and orientation change. *Vision Res.* **14**, 687-692.
- 811 Blake, R., Yu, K., Lokey, M. and Norman, H. (1998) Binocular rivalry and motion perception. *J.*
812 *Cogn. Neurosci.* **10**, 46-60.
- 813 Blakemore, C. and Campbell, F. W. (1969) On the existence of neurones in the human visual
814 system selectively sensitive to the orientation and size of retinal images. *J. Physiol.*
815 *(Lond.)* **203**, 237-260.
- 816 Blakemore, C., Carpenter, R. H. and Georgeson, M. A. (1970) Lateral inhibition between
817 orientation detectors in the human visual system. *Nature* **228**, 37-39.
- 818 Blakemore, C. and Nachmias, J. (1971) The orientation specificity of two visual after-effects. *J.*
819 *Physiol. (Lond.)* **213**, 157-174.
- 820 Blakemore, C. and Sutton, P. (1969) Size of adaptation: a new aftereffect. *Science* **166**,
821 245-247.

- 822 Block, N. (2005) Two neural correlates of consciousness. *Trends Cogn. Sci.* **9**, 46-52.
- 823 Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B. and
824 Dale, A. M. (1998) Functional-anatomic correlates of object priming in humans revealed
825 by rapid presentation event-related fMRI. *Neuron* **20**, 285-296.
- 826 Carlson, T. A. and He, S. (2000) Visible binocular beats from invisible monocular stimuli
827 during binocular rivalry. *Curr. Biol.* **10**, 1055-1058.
- 828 Carpenter, R. H. and Blakemore, C. (1973) Interactions between orientations in human vision.
829 *Exp. Brain Res.* **18**, 287-303.
- 830 Cave, C., Blake, R. and McNamara, T. (1998) Binocular rivalry disrupts visual priming.
831 *Psychol. Sci.* **9**, 299-302.
- 832 Chao, L. L. and Martin, A. (2000) Representation of manipulable man-made objects in the
833 dorsal stream. *Neuroimage* **12**, 478-484.
- 834 Chen, W., Kato, T., Zhu, X. H., Ogawa, S., Tank, D. W. and Ugurbil, K. (1998) Human primary
835 visual cortex and lateral geniculate nucleus activation during visual imagery.
836 *Neuroreport* **9**, 3669-3674.
- 837 Cobb, W. A., Morton, H. B. and Ettlinger, G. (1967) Cerebral Potentials evoked by Pattern
838 Reversal and their Suppression in Visual Rivalry. *Nature* **216**, 1123-1125.
- 839 Corbetta, M. and Shulman, G. L. (2002) Control of goal-directed and stimulus-driven attention
840 in the brain. *Nat. Rev. Neurosci.* **3**, 201-215.
- 841 Craik, F. (1940) Origin of visual after-images. *Nature* **145**, 512.
- 842 Crick, F. and Koch, C. (1995) Are we aware of neural activity in primary visual cortex? *Nature*

843 **375**, 121-123.

844 Culham, J. C., Dukelow, S. P., Vilis, T., Hassard, F. A., Gati, J. S., Menon, R. S. and Goodale,
845 M. A. (1999) Recovery of fMRI activation in motion area MT following storage of the
846 motion aftereffect. *J. Neurophysiol.* **81**, 388-393.

847 de Gelder, B., Vroomen, J., Pourtois, G. and Weiskrantz, L. (1999) Non-conscious recognition
848 of affect in the absence of striate cortex. *Neuroreport* **10**, 3759-3763.

849 De Valois, R. L., Albrecht, D. G. and Thorell, L. G. (1982) Spatial frequency selectivity of cells
850 in macaque visual cortex. *Vision Res.* **22**, 545-559.

851 Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J. and Sergent, C. (2006) Conscious,
852 preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* **10**,
853 204-211.

854 Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J. B., Le Bihan, D. and Cohen, L.
855 (2004) Letter binding and invariant recognition of masked words: behavioral and
856 neuroimaging evidence. *Psychol. Sci.* **15**, 307-313.

857 Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B. and Riviere, D.
858 (2001) Cerebral mechanisms of word masking and unconscious repetition priming. *Nat.*
859 *Neurosci.* **4**, 752-758.

860 Dell'Acqua, R. and Grainger, J. (1999) Unconscious semantic priming from pictures. *Cognition*
861 **73**, B1-B15.

862 Devlin, J. T., Jamison, H. L., Matthews, P. M. and Gonnerman, L. M. (2004) Morphology and
863 the internal structure of words. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 14984-14988.

- 864 DeYoe, E. A. and Van Essen, D. C. (1988) Concurrent processing streams in monkey visual
865 cortex. *Trends Neurosci.* **11**, 219-226.
- 866 Duncan, J. (1984) Selective attention and the organization of visual information. *J. Exp.*
867 *Psychol. Gen.* **113**, 501-517.
- 868 Duong, T. and Freeman, R. D. (2007) Spatial frequency-specific contrast adaptation originates
869 in the primary visual cortex. *J. Neurophysiol.* **98**, 187-195.
- 870 Easton, T. A. (1973) On the normal use of reflexes. *Am. Sci.* **60**, 591-599.
- 871 Eimer, M., Holmes, A. and McGlone, F. P. (2003) The role of spatial attention in the processing
872 of facial expression: an ERP study of rapid brain responses to six basic emotions. *Cogn.*
873 *Affect. Behav. Neurosci.* **3**, 97-110.
- 874 Erdelyi, M. H. (1974) A new look at the new look: perceptual defense and vigilance. *Psychol.*
875 *Rev.* **81**, 1-25.
- 876 Eriksen, C. W. (1960) Discrimination and learning without awareness: a methodological survey
877 and evaluation. *Psychol. Rev.* **67**, 279-300.
- 878 Evans, S. and Azzopardi, P. (2007) Evaluation of a 'bias-free' measure of awareness. *Spat. Vis.*
879 **20**, 61-77.
- 880 Fang, F. and He, S. (2004) Strong influence of test patterns on the perception of motion
881 aftereffect and position. *J. Vis.* **4**, 637-642.
- 882 Fang, F. and He, S. (2005) Cortical responses to invisible objects in the human dorsal and
883 ventral pathways. *Nat. Neurosci.* **8**, 1380-1385.
- 884 Farah, M. J., Wilson, K. D., Drain, M. and Tanaka, J. N. (1998) What is "special" about face

- 885 perception? *Psychol. Rev.* **105**, 482-498.
- 886 Felleman, D. J. and Van Essen, D. C. (1991) Distributed hierarchical processing in the primate
887 cerebral cortex. *Cereb. Cortex* **1**, 1-47.
- 888 Fitzpatrick, D., Lund, J. S. and Blasdel, G. G. (1985) Intrinsic connections of macaque striate
889 cortex: afferent and efferent connections of lamina 4C. *J. Neurosci.* **5**, 3329-3349.
- 890 Flom, M. C., Weymouth, F. W. and Kahneman, D. (1963) Visual resolution and contour
891 interaction. *J. Opt. Soc. Am.* **53**, 1026-1032.
- 892 Fox, R. and Check, R. (1968) Detection of motion during binocular rivalry suppression. *J. Exp.*
893 *Psychol.* **78**, 388-395.
- 894 Fox, R. and Check, R. (1972) Independence between binocular rivalry suppression duration and
895 magnitude of suppression. *J. Exp. Psychol.* **93**, 283-289.
- 896 Frisby, J. P. (1979) *Seeing: Illusion, Brain and Mind*. Oxford University Press: Oxford.
- 897 Gaillard, R., Del Cul, A., Naccache, L., Vinckier, F., Cohen, L. and Dehaene, S. (2006)
898 Nonconscious semantic processing of emotional words modulates conscious access.
899 *Proc. Natl. Acad. Sci. U. S. A.* **103**, 7524-7529.
- 900 Gibson, J. J. (1937) Adaptation, aftereffect, and contrast in the perception of tilted lines. II.
901 simultaneous contrast and the areal restriction of the aftereffect. *J. Exp. Psychol.* **20**,
902 553-569.
- 903 Gibson, J. J. and Radner, M. (1937) Adaptation, aftereffect and contrast in the perception of
904 tilted lines. *J. Exp. Psychol.* **20**, 453-467.
- 905 Gilroy, L. A. and Blake, R. (2005) The interaction between binocular rivalry and negative

906 afterimages. *Curr. Biol.* **15**, 1740-1744.

907 Goebel, R., Muckli, L., Zanella, F. E., Singer, W. and Stoerig, P. (2001) Sustained extrastriate
908 cortical activation without visual awareness revealed by fMRI studies of hemianopic
909 patients. *Vision Res.* **41**, 1459-1474.

910 Goodale, M. A. and Milner, A. D. (1992) Separate visual pathways for perception and action.
911 *Trends Neurosci.* **15**, 20-25.

912 Graham, N. V. S. (1989) *Visual Pattern Analyzers*. Oxford University Press: New York.

913 Green, D. M. and Swets, J. A. (1966) *Signal Detection Theory and Psychophysics*. Wiley: New
914 York.

915 Grill-Spector, K., Henson, R. and Martin, A. (2006) Repetition and the brain: neural models of
916 stimulus-specific effects. *Trends Cogn. Sci.* **10**, 14-23.

917 Grill-Spector, K., Kushnir, T., Edelman, S., Itzchak, Y. and Malach, R. (1998) Cue-invariant
918 activation in object-related areas of the human occipital lobe. *Neuron* **21**, 191-202.

919 Grill-Spector, K., Kushnir, T., Hendler, T. and Malach, R. (2000) The dynamics of
920 object-selective activation correlate with recognition performance in humans. *Nat.*
921 *Neurosci.* **3**, 837-843.

922 Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B., Marinkovic, K. and Rosen, B. R. (1999)
923 Location of human face-selective cortex with respect to retinotopic areas. *Hum. Brain*
924 *Mapp.* **7**, 29-37.

925 Hansen, K. A., Kay, K. N. and Gallant, J. L. (2007) Topographic Organization in and near
926 Human Visual Area V4. *J. Neurosci.* **27**, 11896-11911.

- 927 Haynes, J. D., Deichmann, R. and Rees, G. (2005) Eye-specific effects of binocular rivalry in
928 the human lateral geniculate nucleus. *Nature* **438**, 496-499.
- 929 He, S., Carlson, T. A. and Chen, X. (2005) Parallel pathways and temporal dynamics in
930 binocular rivalry. In: *Binocular Rivalry and Perceptual Ambiguity*. Eds. D. Alais, R.
931 Blake. MIT Press: Cambridge, MA.
- 932 He, S., Cavanagh, P. and Intriligator, J. (1996) Attentional resolution and the locus of visual
933 awareness. *Nature* **383**, 334-337.
- 934 He, S., Cohen, E. R. and Hu, X. (1998) Close correlation between activity in brain area MT/V5
935 and the perception of a visual motion aftereffect. *Curr. Biol.* **8**, 1215-1218.
- 936 He, S. and MacLeod, D. I. (2001) Orientation-selective adaptation and tilt after-effect from
937 invisible patterns. *Nature* **411**, 473-476.
- 938 Holcombe, A. O. and Cavanagh, P. (2001) Early binding of feature pairs for visual perception.
939 *Nat. Neurosci.* **4**, 127-128.
- 940 Holender, D. (1986) Semantic activation without conscious identification in dichotic listening,
941 parafoveal vision, and visual masking: a survey and appraisal. *Behav. Brain Sci.* **9**, 1-66.
- 942 Holmes, A., Vuilleumier, P. and Eimer, M. (2003) The processing of emotional facial expression
943 is gated by spatial attention: evidence from event-related brain potentials. *Brain Res.*
944 *Cogn. Brain Res.* **16**, 174-184.
- 945 Hubel, D. H. (1960) Single unit activity in lateral geniculate body and optic tract of
946 unrestrained cats. *J. Physiol. (Lond.)* **150**, 91-104.
- 947 Hubel, D. H. and Wiesel, T. N. (1962) Receptive fields, binocular interaction and functional

- 948 architecture in the cat's visual cortex. *J. Physiol. (Lond.)* **160**, 106-154.
- 949 Hubel, D. H. and Wiesel, T. N. (1968) Receptive fields and functional architecture of monkey
950 striate cortex. *J. Physiol. (Lond.)* **195**, 215-243.
- 951 Huk, A. C., Ress, D. and Heeger, D. J. (2001) Neuronal basis of the motion aftereffect
952 reconsidered. *Neuron* **32**, 161-172.
- 953 Humphrey, G. K. and Goodale, M. A. (1998) Probing unconscious visual processing with the
954 McCollough effect. *Conscious. Cogn.* **7**, 494-519.
- 955 Ingle, D. (1973) Evolutionary perspectives on the function of the optic tectum. *Brain. Behav.*
956 *Evol.* **8**, 211-237.
- 957 Iwai, E. and Yukie, M. (1987) Amygdalofugal and amygdalopetal connections with
958 modality-specific visual cortical areas in macaques (*Macaca fuscata*, *M. mulatta*, and *M.*
959 *fascicularis*). *J. Comp. Neurol.* **261**, 362-387.
- 960 Jiang, Y., Costello, P., Fang, F., Huang, M. and He, S. (2006) A gender- and sexual
961 orientation-dependent spatial attentional effect of invisible images. *Proc. Natl. Acad. Sci.*
962 *U. S. A.* **103**, 17048-17052.
- 963 Jiang, Y., Costello, P. and He, S. (2007) Processing of invisible stimuli: advantage of upright
964 faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* **18**,
965 349-355.
- 966 Jiang, Y. and He, S. (2006) Cortical responses to invisible faces: dissociating subsystems for
967 facial-information processing. *Curr. Biol.* **16**, 2023-2029.
- 968 Johnson, M. H. (2005) Subcortical face processing. *Nat. Rev. Neurosci.* **6**, 766-774.

- 969 Kanai, R., Tsuchiya, N. and Verstraten, F. A. (2006) The scope and limits of top-down attention
970 in unconscious visual processing. *Curr. Biol.* **16**, 2332-2336.
- 971 Kanwisher, N., McDermott, J. and Chun, M. M. (1997) The fusiform face area: a module in
972 human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**, 4302–4311.
- 973 Kanwisher, N. and Wojciulik, E. (2000) Visual attention: insights from brain imaging. *Nat. Rev.*
974 *Neurosci.* **1**, 91-100.
- 975 Kastner, S., O'Connor, D. H., Fukui, M. M., Fehd, H. M., Herwig, U. and Pinsk, M. A. (2004)
976 Functional imaging of the human lateral geniculate nucleus and pulvinar. *J.*
977 *Neurophysiol.* **91**, 438-448.
- 978 Kastner, S. and Pinsk, M. A. (2004) Visual attention as a multilevel selection process. *Cogn.*
979 *Affect. Behav. Neurosci.* **4**, 483-500.
- 980 Kiefer, M. and Brendel, D. (2006) Attentional modulation of unconscious "automatic"
981 processes: evidence from event-related potentials in a masked priming paradigm. *J.*
982 *Cogn. Neurosci.* **18**, 184-198.
- 983 Kim, C. Y. and Blake, R. (2005) Psychophysical magic: rendering the visible 'invisible'. *Trends*
984 *Cogn. Sci.* **9**, 381-388.
- 985 Koch, C. (2004) *The Quest for Consciousness: a Neuroscientific Approach*. Roberts &
986 Company: Denver, Colorado.
- 987 Koch, C. and Tsuchiya, N. (2007) Attention and consciousness: two distinct brain processes.
988 *Trends Cogn. Sci.* **11**, 16-22.
- 989 Kouider, S. and Dehaene, S. (2007) Levels of processing during non-conscious perception: a

- 990 critical review of visual masking. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **362**,
- 991 857-875.
- 992 Krekelberg, B., Boynton, G. M. and van Wezel, R. J. A. (2006) Adaptation: from single cells to
- 993 BOLD signals. *Trends Neurosci.* **29**, 250-256.
- 994 Kunimoto, C., Miller, J. and Pashler, H. (2001) Confidence and accuracy of near-threshold
- 995 discrimination responses. *Conscious. Cogn.* **10**, 294-340.
- 996 Lachter, J., Forster, K. I. and Ruthruff, E. (2004) Forty-five years after Broadbent (1958): still
- 997 no identification without attention. *Psychol. Rev.* **111**, 880-913.
- 998 Lamme, V. A. (2003) Why visual attention and awareness are different. *Trends Cogn. Sci.* **7**,
- 999 12-18.
- 1000 Lamme, V. A. and Roelfsema, P. R. (2000) The distinct modes of vision offered by feedforward
- 1001 and recurrent processing. *Trends Neurosci.* **23**, 571-579.
- 1002 Lansing, R. W. (1964) Electroencephalographic correlates of binocular rivalry in man. *Science*
- 1003 **146**, 1325-1327.
- 1004 Lavie, N. (1995) Perceptual load as a necessary condition for selective attention. *J. Exp.*
- 1005 *Psychol. Hum. Percept. Perform.* **21**, 451-468.
- 1006 Lavie, N. (2005) Distracted and confused?: selective attention under load. *Trends Cogn. Sci.* **9**,
- 1007 75-82.
- 1008 LeDoux, J. E. (2000) Emotion circuits in the brain. *Annu. Rev. Neurosci.* **23**, 155-184.
- 1009 Lee, S. H., Blake, R. and Heeger, D. J. (2005) Traveling waves of activity in primary visual
- 1010 cortex during binocular rivalry. *Nat. Neurosci.* **8**, 22-23.

- 1011 Lee, T. S. and Nguyen, M. (2001) Dynamics of subjective contour formation in the early visual
1012 cortex. *Proc. Natl. Acad. Sci. U. S. A.* **98**, 1907-1911.
- 1013 Leguire, L. E., Blake, R. and Sloane, M. E. (1981) A novel illusion of bars made from triangles.
1014 *Science* **212**, 1172-1175.
- 1015 Lehmkuhle, S. W. and Fox, R. (1975) Effect of binocular rivalry suppression on the motion
1016 aftereffect. *Vision Res.* **15**, 855-859.
- 1017 Leopold, D. A. and Logothetis, N. K. (1996) Activity changes in early visual cortex reflect
1018 monkeys' percepts during binocular rivalry. *Nature* **379**, 549-553.
- 1019 Li, F. F., VanRullen, R., Koch, C. and Perona, P. (2002) Rapid natural scene categorization in
1020 the near absence of attention. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 9596-9601.
- 1021 Lin, Z. (2007) fMRI adaptation: stimulus specific or processing load specific? *J. Neurosci.* **27**,
1022 11453-11454.
- 1023 Lin, Z. (2008) Unconscious inference and conscious representation: why primary visual cortex
1024 (V1) is directly involved in visual awareness. *Behav. Brain Sci.* **31**, 209-210.
- 1025 Livingstone, M. and Hubel, D. (1988) Segregation of form, color, movement, and depth:
1026 anatomy, physiology, and perception. *Science* **240**, 740-749.
- 1027 Lovibond, P. F. and Shanks, D. R. (2002) The role of awareness in Pavlovian conditioning:
1028 empirical evidence and theoretical implications. *J. Exp. Psychol. Anim. Behav. Process.*
1029 **28**, 3-26.
- 1030 Lumer, E. D., Friston, K. J. and Rees, G. (1998) Neural correlates of perceptual rivalry in the
1031 human brain. *Science* **280**, 1930-1934.

- 1032 Macmillan, N. A. and Creelman, C. D. (1991) *Detection Theory: a User's Guide*. Cambridge
1033 University Press: New York.
- 1034 Maffei, L. and Fiorentini, A. (1973) The visual cortex as a spatial frequency analyser. *Vision*
1035 *Res.* **13**, 1255-1267.
- 1036 Magnussen, S. and Kurtenbach, W. (1980a) Adapting to two orientations: Disinhibition in a
1037 visual aftereffect. *Science* **207**, 908-909.
- 1038 Magnussen, S. and Kurtenbach, W. (1980b) Linear summation of tilt illusion and tilt aftereffect.
1039 *Vision Res.* **20**, 39-42.
- 1040 Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P.
1041 J., Brady, T. J., Rosen, B. R. and Tootell, R. B. (1995) Object-related activity revealed
1042 by functional magnetic resonance imaging in human occipital cortex. *Proc. Natl. Acad.*
1043 *Sci. U. S. A.* **92**, 8135-8139.
- 1044 Mante, V., Frazor, R. A., Bonin, V., Geisler, W. S. and Carandini, M. (2005) Independence of
1045 luminance and contrast in natural scenes and in the early visual system. *Nat. Neurosci.* **8**,
1046 1690-1697.
- 1047 Maruya, K., Yang, E. and Blake, R. (2007) Voluntary action influences visual competition.
1048 *Psychol. Sci.* **18**, 1090-1098.
- 1049 Mather, G., Verstraten, F. and Anstis, S. (1998) *The Motion Aftereffect: A Modern Perspective*.
1050 The MIT Press: Cambridge, MA.
- 1051 McClurkin, J. W. and Marrocco, R. T. (1984) Visual cortical input alters spatial tuning in
1052 monkey lateral geniculate nucleus cells. *J. Physiol. (Lond.)* **348**, 135-152.

- 1053 McCollough, C. (1965) Color adaptation of edge-detectors in the human visual system. *Science*
1054 **149**, 1115-1116.
- 1055 McCormick, P. A. (1997) Orienting attention without awareness. *J. Exp. Psychol. Hum. Percept.*
1056 *Perform.* **23**, 168-180.
- 1057 Melcher, D. and Vidnyanszky, Z. (2006) Subthreshold features of visual objects: unseen but not
1058 unbound. *Vision Res.* **46**, 1863-1867.
- 1059 Merigan, W. H. and Maunsell, J. H. (1993) How parallel are the primate visual pathways? *Annu.*
1060 *Rev. Neurosci.* **16**, 369-402.
- 1061 Merikle, P. M. and Reingold, E. M. (1992) Measuring unconscious perceptual processes. In:
1062 *Perception without Awareness: Cognitive, Clinical, and Social Perspectives.* pp. 55-80.
1063 Eds. R. F. Bornstein, T. S. Pitman. Guilford Press: New York.
- 1064 Merikle, P. M., Smilek, D. and Eastwood, J. D. (2001) Perception without awareness:
1065 perspectives from cognitive psychology. *Cognition* **79**, 115-134.
- 1066 Miller, E. K., Li, L. and Desimone, R. (1991) A neural mechanism for working and recognition
1067 memory in inferior temporal cortex. *Science* **254**, 1377-1379.
- 1068 Miller, J. (1991) The flanker compatibility effect as a function of visual angle, attentional focus,
1069 visual transients, and perceptual load: a search for boundary conditions. *Percept.*
1070 *Psychophys.* **49**, 270-288.
- 1071 Moradi, F., Koch, C. and Shimojo, S. (2005) Face adaptation depends on seeing the face.
1072 *Neuron* **45**, 169-175.
- 1073 Morris, J. S., DeGelder, B., Weiskrantz, L. and Dolan, R. J. (2001) Differential

- 1074 extrageniculostriate and amygdala responses to presentation of emotional faces in a
1075 cortically blind field. *Brain* **124**, 1241-1252.
- 1076 Morris, J. S., Ohman, A. and Dolan, R. J. (1998) Conscious and unconscious emotional learning
1077 in the human amygdala. *Nature* **393**, 467-470.
- 1078 Morris, J. S., Ohman, A. and Dolan, R. J. (1999) A subcortical pathway to the right amygdala
1079 mediating "unseen" fear. *Proc. Natl. Acad. Sci. U. S. A.* **96**, 1680-1685.
- 1080 Morrone, M. C., Burr, D. C. and Maffei, L. (1982) Functional implications of cross-orientation
1081 inhibition of cortical visual cells: I. Neurophysiological evidence. *Proc. R. Soc. Lond. B*
1082 *Biol. Sci.* **216**, 335-354.
- 1083 Naccache, L., Gaillard, R., Adam, C., Hasboun, D., Clemenceau, S., Baulac, M., Dehaene, S.
1084 and Cohen, L. (2005) A direct intracranial record of emotions evoked by subliminal
1085 words. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 7713-7717.
- 1086 Nakamura, K., Dehaene, S., Jobert, A., Le Bihan, D. and Kouider, S. (2005) Subliminal
1087 convergence of Kanji and Kana words: further evidence for functional parcellation of
1088 the posterior temporal cortex in visual word perception. *J. Cogn. Neurosci.* **17**, 954-968.
- 1089 Nakamura, K., Mikami, A. and Kubota, K. (1992) Activity of single neurons in the monkey
1090 amygdala during performance of a visual discrimination task. *J. Neurophysiol.* **67**,
1091 1447-1463.
- 1092 Nguyen, V. A., Freeman, A. W. and Alais, D. (2003) Increasing depth of binocular rivalry
1093 suppression along two visual pathways. *Vision Res.* **43**, 2003-2008.
- 1094 Nishida, S., Ashida, H. and Sato, T. (1997) Contrast dependencies of two types of motion

- 1095 aftereffect. *Vision Res.* **37**, 553-563.
- 1096 O'Connor, D. H., Fukui, M. M., Pinsk, M. A. and Kastner, S. (2002) Attention modulates
1097 responses in the human lateral geniculate nucleus. *Nat. Neurosci.* **5**, 1203-1209.
- 1098 O'Regan, J. K. and Noe, A. (2001) A sensorimotor account of vision and visual consciousness.
1099 *Behav. Brain Sci.* **24**, 939-973.
- 1100 O'Shea, R. P. and Crassini, B. (1981) Interocular transfer of the motion after-effect is not
1101 reduced by binocular rivalry. *Vision Res.* **21**, 801-804.
- 1102 Ohzawa, I., Sclar, G. and Freeman, R. D. (1985) Contrast gain control in the cat's visual system.
1103 *J. Neurophysiol.* **54**, 651-667.
- 1104 Paradiso, M. A., Shimojo, S. and Nakayama, K. (1989) Subjective contours, tilt aftereffects, and
1105 visual cortical organization. *Vision Res.* **29**, 1205-1213.
- 1106 Pare, M. and Wurtz, R. H. (1997) Monkey posterior parietal cortex neurons antidromically
1107 activated from superior colliculus. *J. Neurophysiol.* **78**, 3493-3497.
- 1108 Pasley, B. N., Mayes, L. C. and Schultz, R. T. (2004) Subcortical discrimination of unperceived
1109 objects during binocular rivalry. *Neuron* **42**, 163-172.
- 1110 Perry, V. H., Oehler, R. and Cowey, A. (1984) Retinal ganglion cells that project to the dorsal
1111 lateral geniculate nucleus in the macaque monkey. *Neuroscience* **12**, 1101-1123.
- 1112 Pessoa, L. (2005) To what extent are emotional visual stimuli processed without attention and
1113 awareness? *Curr. Opin. Neurobiol.* **15**, 188-196.
- 1114 Pessoa, L., Japee, S., Sturman, D. and Ungerleider, L. G. (2006) Target visibility and visual
1115 awareness modulate amygdala responses to fearful faces. *Cereb. Cortex* **16**, 366-375.

- 1116 Pessoa, L., Japee, S. and Ungerleider, L. G. (2005) Visual awareness and the detection of
1117 fearful faces. *Emotion* **5**, 243-247.
- 1118 Pessoa, L., Kastner, S. and Ungerleider, L. G. (2002a) Attentional control of the processing of
1119 neural and emotional stimuli. *Brain Res. Cogn. Brain Res.* **15**, 31-45.
- 1120 Pessoa, L., McKenna, M., Gutierrez, E. and Ungerleider, L. G. (2002b) Neural processing of
1121 emotional faces requires attention. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 11458-11463.
- 1122 Plateau, J. (1849) Quatrieme note sur de nouvelles applications curieuses de la persistance des
1123 impressions de la retine. *Bull. Acad. R. Soc. B. A. Belg.* **16**, 254-260.
- 1124 Polonsky, A., Blake, R., Braun, J. and Heeger, D. J. (2000) Neuronal activity in human primary
1125 visual cortex correlates with perception during binocular rivalry. *Nat. Neurosci.* **3**,
1126 1153-1159.
- 1127 Posner, M. I. (1980) Orienting of attention. *Q. J. Exp. Psychol.* **32**, 3-26.
- 1128 Posner, M. I. (1994) Attention: the mechanisms of consciousness. *Proc. Natl. Acad. Sci. U. S. A.*
1129 **91**, 7398-7403.
- 1130 Posner, M. I. and Cohen, Y. (1984) Components of visual orienting. In: *Attention and*
1131 *Performance X: Control of Language Processes*. pp. 531–556. Eds. H. Bouma., D. G.
1132 Bouwhuis. Erlbaum: Hillsdale, NJ.
- 1133 Qian, N., Andersen, R. A. and Adelson, E. H. (1994) Transparent motion perception as
1134 detection of unbalanced motion signals, I. Psychophysics. *J. Neurosci.* **14**, 7357–7366.
- 1135 Rafal, R., Henik, A. and Smith, J. (1991) Extrageniculate contributions to reflex visual orienting
1136 in normal humans: a temporal hemifield advantage. *J. Cogn. Neurosci.* **3**, 322-328.

- 1137 Rajimehr, R. (2004) Unconscious orientation processing. *Neuron* **41**, 663-673.
- 1138 Raymond, J. E., Shapiro, K. L. and Arnell, K. M. (1992) Temporary suppression of visual
1139 processing in an RSVP task: an attentional blink? *J. Exp. Psychol. Hum. Percept.*
1140 *Perform.* **18**, 849-860.
- 1141 Riggs, L. A. and Day, R. H. (1980) Visual aftereffects derived from inspection of orthogonally
1142 moving patterns. *Science* **208**, 416-418.
- 1143 Robinson, D. L. and Petersen, S. E. (1992) The pulvinar and visual salience. *Trends Neurosci.*
1144 **15**, 127-132.
- 1145 Rolls, E. T., Tovee, M. J. and Panzeri, S. (1999) The neurophysiology of backward visual
1146 masking: information analysis. *J. Cogn. Neurosci.* **11**, 300-311.
- 1147 Romanski, L. M. and LeDoux, J. E. (1992) Equipotentiality of thalamo-amygdala and
1148 thalamo-cortico-amygdala circuits in auditory fear conditioning. *J. Neurosci.* **12**,
1149 4501-4509.
- 1150 Schiller, P. H. and Malpeli, J. G. (1978) Functional specificity of lateral geniculate nucleus
1151 laminae of the rhesus monkey. *J. Neurophysiol.* **41**, 788-797.
- 1152 Schneider, W. and Shiffrin, R. M. (1977) Controlled and automatic human information
1153 processing: I. detection, search, and attention. *Psychol. Rev.* **84**, 1-66.
- 1154 Serences, J. T. and Yantis, S. (2006) Selective visual attention and perceptual coherence. *Trends*
1155 *Cogn. Sci.* **10**, 38-45.
- 1156 Shapley, R. and Enroth-Cugell, C. (1984) Visual adaptation and retinal gain controls. *Prog.*
1157 *Retin. Res.* **3**, 263-346.

- 1158 Sheinberg, D. L. and Logothetis, N. K. (1997) The role of temporal cortical areas in perceptual
1159 organization. *Proc. Natl. Acad. Sci. U. S. A.* **94**, 3408-3413.
- 1160 Shimojo, S., Kamitani, Y. and Nishida, S. (2001) Afterimage of perceptually filled-in surface.
1161 *Science* **293**, 1677-1680.
- 1162 Shipp, S. (2004) The brain circuitry of attention. *Trends Cogn. Sci.* **8**, 223-230.
- 1163 Siegel, S. and Allan, L. G. (1992) Pairings in learning and perception: Pavlovian conditioning
1164 and contingent aftereffects. In: *The Psychology of Learning and Motivation: Advances*
1165 *in Research and Theory*. pp. 127-160. Ed. D. Medin. Academic Press: San Diego, CA.
- 1166 Sillito, A. M., Jones, H. E., Gerstein, G. L. and West, D. C. (1994) Feature-linked
1167 synchronization of thalamic relay cell firing induced by feedback from the visual cortex.
1168 *Nature* **369**, 479-482.
- 1169 Sincich, L. C., Park, K. F., Wohlgenuth, M. J. and Horton, J. C. (2004) Bypassing V1: a direct
1170 geniculate input to area MT. *Nat. Neurosci.* **7**, 1123-1128.
- 1171 Snowden, R. J. and Verstraten, F. A. J. (1999) Motion transparency: making models of motion
1172 perception transparent. *Trends Cogn. Sci.* **3**, 369-377.
- 1173 Solomon, S. G., Peirce, J. W., Dhruv, N. T. and Lennie, P. (2004) Profound contrast adaptation
1174 early in the visual pathway. *Neuron* **42**, 155-162.
- 1175 Stefanacci, L. and Amaral, D. G. (2002) Some observations on cortical inputs to the macaque
1176 monkey amygdala: an anterograde tracing study. *J. Comp. Neurol.* **451**, 301-323.
- 1177 Steriade, M. and Deschenes, M. (1984) The thalamus as a neuronal oscillator. *Brain Res.* **320**,
1178 1-63.

- 1179 Tanaka, K. (1996) Inferotemporal cortex and object vision. *Annu. Rev. Neurosci.* **19**, 109-139.
- 1180 Tanaka, K. (1997) Mechanisms of visual object recognition: monkey and human studies. *Curr.*
1181 *Opin. Neurobiol.* **7**, 523-529.
- 1182 Theoret, H., Kobayashi, M., Ganis, G., Di Capua, P. and Pascual-Leone, A. (2002) Repetitive
1183 transcranial magnetic stimulation of human area MT/V5 disrupts perception and storage
1184 of the motion aftereffect. *Neuropsychologia* **40**, 2280-2287.
- 1185 Tong, F. and Engel, S. A. (2001) Interocular rivalry revealed in the human cortical blind-spot
1186 representation. *Nature* **411**, 195-199.
- 1187 Tong, F., Meng, M. and Blake, R. (2006) Neural bases of binocular rivalry. *Trends Cogn. Sci.*
1188 **10**, 502-511.
- 1189 Tong, F., Nakayama, K., Vaughan, J. T. and Kanwisher, N. (1998) Binocular rivalry and visual
1190 awareness in human extrastriate cortex. *Neuron* **21**, 753-759.
- 1191 Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., Brady, T. J.
1192 and Rosen, B. R. (1995) Visual motion aftereffect in human cortical area MT revealed
1193 by functional magnetic resonance imaging. *Nature* **375**, 139-141.
- 1194 Treisman, A. (1996) The binding problem. *Curr. Opin. Neurobiol.* **6**, 171-178.
- 1195 Treisman, A. (1999) Solutions to the binding problem: progress through controversy and
1196 convergence. *Neuron* **24**, 105-110, 111-125.
- 1197 Tsuchiya, N. and Koch, C. (2005) Continuous flash suppression reduces negative afterimages.
1198 *Nat. Neurosci.* **8**, 1096-1101.
- 1199 Tsuchiya, N., Koch, C., Gilroy, L. A. and Blake, R. (2006) Depth of interocular suppression

1200 associated with continuous flash suppression, flash suppression, and binocular rivalry. *J.*
1201 *Vis.* **6**, 1068-1078.

1202 Tyler, L. K., Russell, R., Fadili, J. and Moss, H. E. (2001) The neural representation of nouns
1203 and verbs: PET studies. *Brain* **124**, 1619-1634.

1204 Ungerleider, L. G. and Mishkin, M. (1982) Two cortical visual systems. In: *Analysis of Visual*
1205 *Behavior*. Eds. D. J. Ingle., M. A. Goodale., R. J. W. Mansfield. MIT Press: Cambridge,
1206 MA.

1207 van der Zwan, R. and Wenderoth, P. (1994) Psychophysical evidence for area V2 involvement
1208 in the reduction of subjective contour tilt aftereffects by binocular rivalry. *Vis. Neurosci.*
1209 **11**, 823-830.

1210 van der Zwan, R., Wenderoth, P. and Alais, D. (1993) Reduction of a pattern-induced motion
1211 aftereffect by binocular rivalry suggests the involvement of extrastriate mechanisms. *Vis.*
1212 *Neurosci.* **10**, 703-709.

1213 Verstraten, F. A. J., Fredericksen, R. E. and van de Grind, W. A. (1994) The motion aftereffect
1214 of bi-vectorial transparent motion. *Vision Res.* **34**, 349-358.

1215 Volker, T., Lin, Z. and Lavie, N. (under review) The role of perceptual load in object
1216 recognition.

1217 Vuilleumier, P., Armony, J. L., Driver, J. and Dolan, R. J. (2001) Effects of attention and
1218 emotion on face processing in the human brain: an event-related fMRI study. *Neuron* **30**,
1219 1-20.

1220 Vuilleumier, P., Armony, J. L., Driver, J. and Dolan, R. J. (2003) Distinct spatial frequency

- 1221 sensitivities for processing faces and emotional expressions. *Nat. Neurosci.* **6**, 624-631.
- 1222 Wade, N. J. (1998) *A Natural History of Vision*. MIT Press: Cambridge MA.
- 1223 Wade, N. J. and Wenderoth, P. (1978) The influence of colour and contour rivalry on the
1224 magnitude of the tilt aftereffect. *Vision Res.* **18**, 827-835.
- 1225 Wales, R. and Fox, R. (1970) Increment detection thresholds during binocular rivalry
1226 suppression. *Percept. Psychophys.* **8**, 90-94.
- 1227 Webster, M. J., Ungerleider, L. G. and Bachevalier, J. (1991) Connections of inferior temporal
1228 areas TE and TEO with medial temporal-lobe structures in infant and adult monkeys. *J.*
1229 *Neurosci.* **11**, 1095-1116.
- 1230 Weiskrantz, L. (1997) *Consciousness Lost and Found: a Neuropsychological Exploration*.
1231 Oxford University Press: Oxford.
- 1232 Wenderoth, P. and Johnstone, S. (1987) Possible neural substrates for orientation analysis and
1233 perception. *Perception* **16**, 693-709.
- 1234 Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B. and Jenike, M. A. (1998)
1235 Masked presentations of emotional facial expressions modulate amygdala activity
1236 without explicit knowledge. *J. Neurosci.* **18**, 411-418.
- 1237 White, K. D., Petry, H. M., Riggs, L. A. and Miller, J. (1978) Binocular interactions during
1238 establishment of McCollough effects. *Vision Res.* **18**, 1201-1215.
- 1239 Wiens, S. and Ohman, A. (2002) Unawareness is more than a chance event: comment on
1240 Lovibond and Shanks (2002). *J. Exp. Psychol. Anim. Behav. Process.* **28**, 27-31.
- 1241 Wiesenfelder, H. and Blake, R. (1990) The neural site of binocular rivalry relative to the

- 1242 analysis of motion in the human visual system. *J. Neurosci.* **10**, 3880-3888.
- 1243 Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F. and Mattingley, J. B. (2004)
- 1244 Amygdala responses to fearful and happy facial expressions under conditions of
- 1245 binocular suppression. *J. Neurosci.* **24**, 2898-2904.
- 1246 Woldorff, M. G., Gallen, C. C., Hampson, S. A., Hillyard, S. A., Pantev, C., Sobel, D. and
- 1247 Bloom, F. E. (1993) Modulation of early sensory processing in human auditory cortex
- 1248 during auditory selective attention. *Proc. Natl. Acad. Sci. U. S. A.* **90**, 8722-8726.
- 1249 Wolfe, J. M. and Cave, K. R. (1999) The psychophysical evidence for a binding problem in
- 1250 human vision. *Neuron* **24**, 11-17, 111-125.
- 1251 Wunderlich, K., Schneider, K. A. and Kastner, S. (2005) Neural correlates of binocular rivalry
- 1252 in the human lateral geniculate nucleus. *Nat. Neurosci.* **8**, 1595-1602.
- 1253 Yang, E., Zald, D. H. and Blake, R. (2007) Fearful expressions gain preferential access to
- 1254 awareness during continuous flash suppression. *Emotion* **7**, 882-886.
- 1255 Yantis, S. and Johnston, J. C. (1990) On the locus of visual selection: evidence from focused
- 1256 attention tasks. *J. Exp. Psychol. Hum. Percept. Perform.* **16**, 135-149.
- 1257 Yantis, S. and Jonides, J. (1984) Abrupt visual onsets and selective attention: evidence from
- 1258 visual search. *J. Exp. Psychol. Hum. Percept. Perform.* **10**, 601-621.
- 1259 Zald, D. H. (2003) The human amygdala and the emotional evaluation of sensory stimuli. *Brain*
- 1260 *Res. Brain Res. Rev.* **41**, 88-123.
- 1261 Zimba, L. D. and Blake, R. (1983) Binocular rivalry and semantic processing: out of sight, out
- 1262 of mind. *J. Exp. Psychol. Hum. Percept. Perform.* **9**, 807-815.

1263 Table 1

1264 *Level of unconscious processing during binocular rivalry (BR) and continuous flash*

1265 *suppression (CFS) as measured by strength of aftereffect (AE) after adaptation*

Type of adaptation	Adaptor	Level of processing
Afterimages (AIs)	Gray gratings during BR	<i>Reduced</i> strength (Gilroy & Blake, 2005)
	Color gratings during CFS	<i>Reduced</i> strength: the more completely the adaptor was suppressed, the more strongly the AI intensity was reduced (Tsuchiya & Koch, 2005)
Tilt after-effects (TAEs)	Gratings inclined 10 or 15° from the vertical during BR	<i>Full</i> strength (Wade & Wenderoth, 1978)
Spatial frequency aftereffects	Square wave gratings during BR	<i>Full</i> strength: Magnitude as measured by contrast threshold elevation and spatial frequency shift was determined solely by

		stimulus duration and independent of awareness (Blake & Fox, 1974)
	Sinusoidal wave gratings during BR	<i>Full</i> strength for high-contrast adaptors, reduced strength for low-contrast adaptors, as measured by contrast threshold elevation (Blake et al., 2006)
Color aftereffects (CAEs)	Color gratings during BR	<i>Full</i> strength (White et al., 1978)
Motion aftereffects (MAEs)	Translational motion during BR	<i>Full</i> strength (Wade & Wenderoth, 1978); interocular transfer of the MAE is not reduced by awareness (O'Shea & Crassini, 1981); <i>full</i> strength for high-contrast adaptors, <i>reduced</i> strength

for low-contrast adaptors

(Blake et al., 2006)

Rotating spiral during BR *Reduced* strength:

magnitude was

proportional to the total

duration of spiral visibility

during adaptation

(Wiesenfelder & Blake,

1990);

Drifting plaid during BR *Reduced* strength (van der

Zwan et al., 1993)

1266 *Note.* For an introduction to adaptation, see Box 2; for definitions of the AEs mentioned, see

1267 Box 3

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1276 **Box 1. Measures of awareness**

1277 The notion that consciousness reflects *subjective* experience is central to nearly all theories of
1278 consciousness. On the other hand, the scientific quest for perception without awareness and its
1279 neural correlates requires establishing *objective* unawareness of the stimuli. In fact, the lack of
1280 an accepted measure of awareness has made any claim of perception without awareness
1281 controversial. We believe that to be objective, measures should be both *reliable* and *valid* (cf.
1282 Lovibond and Shanks, 2002). To be reliable, measures should not be contaminated by demand
1283 characteristics (i.e. an experimental artifact where observers change their behavior to conform
1284 to the experimenter's expectations) or response bias (e.g. individual differences in reporting
1285 thresholds). To be valid, measures should truly tap into the presumed theoretical construct of
1286 awareness. In other words, assessment should be both relevant and sensitive to the question
1287 being investigated; at the same time, assessment should be sensitive only to aware but not
1288 unaware processes (Merikle and Reingold, 1992; Wiens and Ohman, 2002).

1289
1290 In practice, measures of awareness can be classified into two types: subjective (e.g. self-report)
1291 and objective (e.g. forced-choice). In subjective measurement, report of seeing (or not seeing)
1292 the stimuli is taken as being aware (or unaware) of the stimuli; in objective measurement, better
1293 than chance (or around chance) performance in discriminating between alternative stimuli is
1294 regarded as being aware (or unaware) of the stimuli (Merikle *et al.*, 2001). Subjective measures,
1295 albeit intrinsic to the concept of awareness, are potentially confounded by response bias (Green
1296 and Swets, 1966; Macmillan and Creelman, 1991): people who are under-confident tend to set

1297 up a high criterion and report stimuli invisible even when the stimuli are above visibility
1298 thresholds, making it an unreliable measurement. Instead, forced-choice procedures, which
1299 yield more criterion-independent measures of awareness, are routinely used in the quest for
1300 neural correlates of awareness (Eriksen, 1960; Holender, 1986). At the same time, to preserve
1301 the merits of subjective measures while avoiding confounds (e.g. subjective criteria), it is also
1302 of merits to use signal detection theory to characterize behavioral performance with receiver
1303 operating characteristic curves in detection task (Evans and Azzopardi, 2007; Kunimoto *et al.*,
1304 2001; Pessoa *et al.*, 2005). In general, for studies strongly based on the prerequisite that the
1305 stimuli are invisible, objective measures of awareness should be used. Moreover, validity issues
1306 should be considered carefully.

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1318 **Box 2. The neural mechanism of adaptation and its application in the quest for the neural**
1319 **correlates of consciousness**

1320 Sensory systems are constantly adapting to changes in the environment and adjusting their
1321 sensitivities accordingly. In fact, it is such a ubiquitous property that it occurs at multiple stages
1322 of processing and has been studied with multiple techniques, ranging from psychophysics to
1323 single unit recordings (Miller *et al.*, 1991) and fMRI (Buckner *et al.*, 1998). When measured
1324 with psychophysics, visual adaptation refers to the phenomenon that prolonged exposure to a
1325 visual stimulus (i.e. adaptor) alters the visual system's sensitivity to, or the appearance of a
1326 subsequent related stimulus (i.e. test), with the altered appearance called visual *aftereffect* (AE).
1327 When measured with fMRI, adaptation refers to the observation of decreased neural activity for
1328 repeated versus novel stimuli (i.e. fMRI adaptation; for reviews see Krekelberg *et al.*, 2006; Lin,
1329 2007). Specifically, adaptation is termed *pattern adaptation* if an effective pattern (e.g. tilt)
1330 serves as an adaptor to reduce the responsiveness to a subsequent test, and termed *contrast*
1331 *adaptation* if an effective contrast image (usually a high contrast one) serves as an adaptor to
1332 reduce contrast sensitivity to a subsequent test. A special category of AE, called afterimage (AI),
1333 does not require a particular test to observe the effect; in other words, an image continues to
1334 appear in one's vision after the original image has ceased.

1335
1336 What is the neural mechanism of adaptation? Generally, adaptation to bright environment and
1337 dark environment (i.e. light adaptation and dark adaptation, respectively) is believed to occur
1338 entirely in the retina (Shapley and Enroth-Cugell, 1984). Similarly, negative AI (see also Box 3f)

1339 is largely attributed to retinal mechanisms with some contributions of post-retinal process (e.g.
1340 Shimojo *et al.*, 2001). Yet, there are at least two reasons to believe that, in general, AE due to
1341 pattern and contrast adaptation is mainly a cortical phenomenon with some limited subcortical
1342 contributions (for a review, see Graham, 1989). First, AE in one eye affects response to
1343 un-adapted stimulus presented to the other eye (Gibson, 1937), implying a binocular
1344 mechanism. Although neurons in the lateral geniculate nucleus (LGN) display interocular
1345 transfer of information (e.g. with their receptive field surrounds, McClurkin and Marrocco,
1346 1984; Sillito *et al.*, 1994), and the LGN is reciprocally connected to other thalamic nuclei that
1347 contain binocular neurons (e.g. the perigeniculate nucleus, Steriade and Deschenes, 1984),
1348 excitatory binocular processing within the geniculocortical pathway occurs first in primary
1349 visual cortex (V1, Hubel, 1960). Second, AE is orientation specific such that a horizontal
1350 adapting grating does not influences the threshold or the apparent spatial frequency of vertical
1351 test gratings (Blakemore and Nachmias, 1971). Critically, orientation selectivity and tuning is
1352 not found before V1 (Hubel and Wiesel, 1962, 1968). Thus, AE has been used to infer the
1353 properties of cortical feature analyzers (Gibson and Radner, 1937). On the other hand, AE does
1354 have some subcortical mechanisms. For instance, most neurons in the LGN still show
1355 adaptation to contrasts of drifting sinusoidal gratings, albeit to a lesser degree than neurons in
1356 visual cortex (Ohzawa *et al.*, 1985). More strikingly, a recent study of the macaque monkeys
1357 found that magnocellular (but not parvocellular) LGN neurons showed strong contrast
1358 adaptation that originated in the ganglion cells, pushing the mechanisms of contrast adaptation
1359 to subcortical pathways (Solomon *et al.*, 2004; but see Mante *et al.*, 2005). That said, spatial

1360 frequency specific contrast adaptation and presumably other types of pattern specific visual
1361 adaptation is still believed to origin in V1 (Duong and Freeman, 2007), which is selective for
1362 visual features such as orientation, direction, position, and speed. For example, it has been
1363 shown that neural activity in V1 is substantially reduced after a few seconds of visual
1364 stimulation with an effective pattern, which is thought to be the neural substrate of a variety of
1365 perceptual AE. Similarly, *motion adaptation* in motion area V5 (Culham *et al.*, 1999; He *et al.*,
1366 1998; Theoret *et al.*, 2002; Tootell *et al.*, 1995) and early visual areas (V1, V2 and V3, which
1367 possess direction-selective neurons, Huk *et al.*, 2001) are thought to be responsible for motion
1368 AE.

1369
1370 Based on its neural underpinnings, adaptation, “the psychologist’s microelectrode” (Frisby,
1371 1979), acts as a probe for inferring the relative contributions of V1 and other visual areas in
1372 visual awareness (e.g. orientation-selective adaptation, He *et al.*, 1996; He and MacLeod, 2001).
1373 Specifically, when similar or equal strength of adaptation is found for visible and invisible
1374 inputs, neural correlates of such unperturbed adaptation are inferred as uncorrelated with visual
1375 awareness.

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1381 **Box 3. The variety of visual aftereffects**

1382 There are numerous kinds of visual aftereffects (AEs). Throughout this article, we mention
1383 several of them in the context of binocular rivalry (BR) and continuous flash suppression (CFS).
1384 Understanding these AEs is important to appreciate how they serve as tools in probing the depth
1385 of unconscious processing. Toward that end, we describe several important AEs below in order
1386 of their appearance in the text. In addition, we have prepared a webpage with demonstrations.
1387 The URL for that webpage is <http://zhichenglin.googlepages.com/demonstrations>.

1388

1389 **1. Tilt aftereffect (TAE)**

1390 Prolonged adaptation to an oriented visual stimulus causes a subsequent image to appear
1391 repulsed away from the adapting orientation (Gibson and Radner, 1937). For example, after
1392 prolonged viewing of an inclined grating, a vertically presented test grating appears as tilted in
1393 the opposite direction. It also occurs after adaptation to illusory contour tilt (Paradiso *et al.*,
1394 1989). TAE is believed to occur as a result of altered patterns of activity in orientation-selective
1395 neurons in V1 and V2, most likely due to inhibitory interactions (Blakemore *et al.*, 1970;
1396 Carpenter and Blakemore, 1973; Magnussen and Kurtenbach, 1980a, b; Morrone *et al.*, 1982;
1397 Wenderoth and Johnstone, 1987).

1398

1399 **2. Spatial frequency aftereffect**

1400 This comes in two forms: contrast threshold elevation and spatial frequency shift. *Contrast*
1401 *threshold elevation* is measured in contrast sensitivity function (CSF, Blakemore and Campbell,

1402 1969). CSF is determined by finding the contrast threshold (i.e. the minimal amount of contrast
1403 needed to make a grating look striped) at different spatial frequencies; a typical finding is that
1404 the threshold is lowest (i.e. sensitivity is highest) at intermediate spatial frequencies, around 4
1405 to 5 cycles per degree of visual angle. After prolonged exposure to a high contrast grating of a
1406 particular spatial frequency, more contrast is required (i.e. contrast threshold is elevated) to be
1407 able to detect a grating of the same spatial frequency than before adaptation, with contrast
1408 thresholds for quite different spatial frequencies being unaffected. In other words, the minimal
1409 intensity difference between light and dark bars to enable detection of a grating is elevated. This
1410 is called contrast threshold elevation and occurs only for gratings similar to the adapting pattern
1411 in orientation. On the other hand, *spatial frequency shift* (Blakemore and Sutton, 1969) refers to
1412 the finding that prolonged adaptation to a high-contrast grating causes a subsequent grating
1413 shift away from the adapting spatial frequency—a grating with spatial frequency higher (or
1414 lower) than that of the adaptor appear with even higher (or lower) spatial frequency than it
1415 actually is. The AE is generally accepted as due to neural activity in V1/V2 (De Valois *et al.*,
1416 1982; Maffei and Fiorentini, 1973).

1417

1418 **3. Orientation-contingent color aftereffect (a.k.a. the McCollough effect)**

1419 In the McCollough effect (McCollough, 1965), prolonged exposure to a pair of colored gratings
1420 (e.g. a vertical green grating and a horizontal red grating) causes a pair of colorless gratings
1421 appear tinged with the opposite color contingent on the orientation of the adapting gratings and
1422 the test gratings (e.g. the vertical grating appears reddish whereas the horizontal grating appears

1423 greenish). The AE can last for a long time, but it requires a period of adaptation to manifest.
1424 Although its exact neural mechanisms are still disputed, accumulating evidence suggests that
1425 they might be located early in the cortical visual pathways, probably in V1 (e.g. Humphrey and
1426 Goodale, 1998; but see Siegel and Allan, 1992 for an associative learning explanation).

1427

1428 **4. Motion aftereffect (MAE)**

1429 Prolonged adaptation to a regularly moving stimulus renders a subsequent physically stationary
1430 test pattern to appear to move in the opposite direction (Addams, 1834; Mather *et al.*, 1998).

1431 Known as MAE, it usually comes in several forms. One type is called the translational (i.e.

1432 linear) MAE. A well know example is the waterfall illusion: prolonged viewing of a waterfall

1433 makes subsequent stationary rocks besides the fall appear moving upward. Whether the

1434 translational MAE reflects low-level or high-level motion mechanisms depends on the nature of

1435 the test pattern: MAE measured with a dynamic test pattern is considered to reflect higher

1436 stages of motion processing than MAE measured with a static test pattern (Fang and He, 2004;

1437 Nishida *et al.*, 1997). Another type of MAE is the spiral AE (Plateau, 1849): after adaptation to

1438 a rotating spiral, a subsequent stationary spiral (or other stationary patterns) appears to move in

1439 the opposite directions. Still another type of MAE is plaid-induced MAE: motion stimuli

1440 composed of moving gratings of different orientations are perceived as a coherent plaid pattern

1441 moving in a single direction and speed. Prolonged exposure to such moving plaid pattern can

1442 also generate MAE similar to translational MAE. A related type of MAE is the transparent

1443 MAE: bivectorial motion stimuli composed of two sets of randomly positioned dots moving in

1444 different directions and at different speeds are perceived as two overlapping surfaces moving
1445 transparently over each other (however, if the dots are locally paired, the two dot fields are not
1446 segmented into two separate surfaces but perceived as a single surface moving with the vector
1447 average velocity of the two component vectors, Qian *et al.*, 1994; Snowden and Verstraten,
1448 1999). Adaptation to such transparent motion results in a direction inverse of the vector sum of
1449 both inducing patterns (Riggs and Day, 1980; Verstraten *et al.*, 1994). In general, the neural
1450 mechanisms of MAE include area V5 (Culham *et al.*, 1999; He *et al.*, 1998; Theoret *et al.*, 2002;
1451 Tootell *et al.*, 1995) and early visual areas (V1, V2 and V3, which possess direction-selective
1452 neurons, Huk *et al.*, 2001).

1453

1454 **5. Square-wave illusion aftereffect**

1455 In a triangular-wave spatial luminance grating, the locations of peak luminance appear as thin,
1456 bright stripes, with luminance falling off gradually and symmetrically on both sides of these
1457 peaks. After a few moments of adaptation, however, alternating light and dark illusory bars
1458 appear to be illuminated from either the right or left, resembling a square-wave grating with
1459 rounded edges (Leguire *et al.*, 1981). In other words, adaptation renders a triangular-wave
1460 grating to appear like a square-wave grating. It may reflect the operation of cortical
1461 phase-selective mechanisms.

1462

1463 **6. Negative afterimages**

1464 After exposure to an image, an illusory percept continues to appear in one's vision although the

1465 original one has ceased (Craik, 1940). Known as afterimage (AI), it usually comes in two types:
1466 positive AI and negative AI. In positive AI, bright areas remain bright and dark areas remain
1467 dark; in negative AI, however, bright areas turn dark and dark areas turn bright. Much research
1468 has been done in negative AI. Similar to color AE, if the adaptor is a saturated color, then
1469 adaptation to it will generate an illusory percept of the complementary color at a uniform gray
1470 field. Unlike color AE, however, most AI lasts for only a few seconds to a minute: positive AI,
1471 thought to be associated with retinal latency, last only for tens of milliseconds; negative AI,
1472 attributed to photoreceptor fatigue due to photopigment bleaching, can last longer (e.g. tens of
1473 seconds). Negative AI is largely due to retinal mechanisms with some contributions of
1474 post-retinal process (e.g. Shimojo *et al.*, 2001).

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1486 **Box 4. The parvocellular and magnocellular pathways**

1487 Anatomically, the parvo and magno cells in the lateral geniculate nucleus (LGN) originate from
1488 morphologically distinct retinal ganglion cells, midget cells and parasol cells, respectively
1489 (Perry *et al.*, 1984). Coincidentally, the first letters of *parvo* and *magno* cells and their
1490 corresponding *midget* and *parasol* cells are in exact reverse. So, a potential confusion is that
1491 when one refers to the M system it is unclear whether one is referring to the midget or magno
1492 cell. The convention is to use P and M to refer to parvo and magno, respectively. The names of
1493 the channels derive from the relative sizes of the cells in the segregated laminae of the dorsal
1494 LGN (dLGN) to which they project—P cells have small cell bodies, thin axons, and slow
1495 axonal conduction speed, whereas M cells have large cell bodies, thick axons, and fast axonal
1496 conduction speed (Schiller and Malpeli, 1978). The P and M pathways are segregated in the
1497 LGN between its four dorsal layers and two ventral layers, respectively. This segregation
1498 continues up to primary visual cortex (V1), with the P pathway terminating primarily in layers
1499 4A and 4Cb and the M pathway in layer 4Ca and 6 (Fitzpatrick *et al.*, 1985). The P and M
1500 pathways are preferentially associated the ventral and dorsal cortical pathways, respectively;
1501 however, they are not confined exclusively to either pathway (Felleman and Van Essen, 1991;
1502 Merigan and Maunsell, 1993). For example, visual cortical area 4 (V4), including its ventral
1503 and dorsal parts (Hansen *et al.*, 2007), receives a mixed input from both the M and P systems.
1504 Besides these geniculo-striate pathways, it should be noted that the dorsal stream, especially the
1505 posterior parietal cortex (Pare and Wurtz, 1997), also receives visual input from the superior
1506 colliculus (SC) through the pulvinar (i.e. a subcortical projection).

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Functionally, the P pathway is color sensitive, is tuned to higher spatial frequencies, is sensitive to lower temporal frequencies, and has lower contrast sensitivity; the M channel responds very poorly to isoluminant stimuli, even when moving, but is responsive to lower spatial frequencies, is sensitive to higher temporal frequencies, and has higher contrast sensitivity (Schiller and Malpeli, 1978). Thus, a common strategy to preferentially activate either pathway is to stimulate the P pathway with stimuli that are defined in color or have high spatial frequency, and the M pathway with stimuli that have low contrast or spatial frequency. However, it should be noted that in reality responses of the two pathways to most visual stimuli overlap significantly; one has to go to the very extremes of the response spectrum to get good differential activation. Additionally, although P cells have low contrast sensitivity, a high contrast stimulus will not activate them preferentially (M cells respond well to high contrasts). Similarly, low temporal frequencies or high luminance (rather than isoluminant) stimuli will not evoke preferential activation of P cells (the M system has high sensitivity and it continues to respond to isoluminance at low spatial frequencies albeit at a reduced rate). Moreover, stimuli that may preferentially activate individual P or M cells do not necessarily preferentially activate the P or M cell populations as a whole. For example, although individual P cells have lower contrast sensitivity than individual M cells, collectively they match the performance of M cells because there are so many more of them. For this reason, an M-cell lesion will not reduce behavioral contrast sensitivity (J. H. R. Maunsell, personal communication, December 10, 2007).

1528 **Box 5. Selective attention in the brain**

1529 Efficient computation of perceptual priority is a hallmark of adaptive behavior for at least two
1530 reasons. First, while sensory inputs are massive, attention capacity is limited. Competition for
1531 limited representational resources calls for a gating mechanism to prioritize relevant information
1532 and thus reduce information overload. Such competition is biased not only by sensory saliency,
1533 whose weight decreases in the neural hierarchy, but also by visual attention, whose weight
1534 increases in the hierarchy (Kastner and Pinsk, 2004; O'Connor *et al.*, 2002; Serences and Yantis,
1535 2006). Second, to interpret sensory inputs, it is necessary to first assign features to either figure
1536 or ground and then integrate multiple features across space and time for perceptual coherence.
1537 This is further constrained by the distinct preferences of neurons in the hierarchy: neurons in
1538 early visual areas respond to small areas of visual space (receptive fields, RFs) and code simple
1539 features (e.g. orientation and spatial frequency), whereas neurons in later areas have large RFs
1540 and code more complex features. Attention serves to integrate distributed neural representations
1541 of features to form coherent object representations (Treisman, 1996). Two distinct forms of
1542 attention subserve such adaptive behavior. A knock on the door, for example, may distract you
1543 from focusing on the paper; or you may decide to check the time since a meeting is coming up.
1544 The former, that salient events (e.g. transient changes in luminance or contrast) capture attention,
1545 is termed bottom-up (or transient /stimulus-driven/exogenous/reflexive) attention; the latter, that
1546 goal and expectation drives attention, is dubbed top-down (or
1547 sustained/goal-driven/endogenous/voluntary) attention. Although orienting of attention is usually
1548 accompanied by eye movements (i.e. overt attention), covert orienting of attention without eye

1549 movements is possible especially in laboratory settings (Posner, 1980).

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1551 Given its important role in performing a variety of tasks, it won't be surprising that attention is

1552 not a single entity, but a set of cortical and subcortical processes that interact mutually. First, at

1553 the cortical level, the source of top-down and bottom-up attention is generally believed to

1554 comprise two networks: 1) top-down attention originates from the dorsal posterior parietal cortex

1555 (e.g. the intraparietal sulcus) and the frontal cortex (e.g. the frontal eye field), forming the

1556 so-called *dorsal frontoparietal network*; 2) bottom-up attention stems from the temporoparietal

1557 junction and the ventral frontal cortex (largely lateralized to the right hemisphere), constituting

1558 the so-called *ventral frontoparietal network* (Corbetta and Shulman, 2002). Second, at the

1559 subcortical level, several regions have been identified to be important for control of attention.

1560 For example, the visual grasp reflex—reflexively orienting the eyes toward salient events in the

1561 visual periphery—is supported by the phylogenetically primitive *midbrain circuits* in all

1562 vertebrates (Ingle, 1973). Later studies pinpointed that the superior colliculus (SC) in the

1563 midbrain and the pulvinar in the thalamus are important for both overt and covert attention.

1564 Specifically, retinal projection to the SC is critical for attentional orienting and involuntary

1565 capture of attention (Rafal *et al.*, 1991). Besides, the amygdala also plays an important role in

1566 orienting attention by projecting to cholinergic and noradrenergic cells, which are capable of

1567 exerting widespread effects on attention (Aston-Jones *et al.*, 1999), and to cells in cortical

1568 sensory regions (Amaral *et al.*, 1992). Third, the cortical and subcortical attention networks

1569 interact a lot; attentional selectivity can be achieved through an orchestration of subcortical

1570 reflex circuits by cortical processes that can activate or inhibit them (Easton, 1973). Indeed,
1571 anatomically the subcortical and cortical attention areas are inter- and intra-connected. For
1572 instance, the SC receives direct descending inputs from cortical visual areas and the dorsal
1573 frontoparietal network; it returns its outputs through numerous thalamic sites including the visual
1574 components of the thalamus (e.g. the LGN and the pulvinar). On the other hand, the pulvinar
1575 (especially its ventral division) receives its major inputs from the visual cortex and returns its
1576 total outputs to the cortex, serving as a hub for cortico-cortical communication (for a review, see
1577 Shipp, 2004). Note that the dorsal pulvinar (similar to the “medial pulvinar” of histological brain
1578 atlases) has connections with the cingulate, frontal, and (auditory) superior temporal areas, so its
1579 range of inputs is probably just as diverse as those to the SC (S. Shipp, personal communication,
1580 December 11, 2007).

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1591 **Box 6. Unattended versus irrelevant stimuli**

1592 In attention literature, it is crucial to distinguish *unattended* stimuli from *irrelevant*
1593 stimuli—irrelevant stimuli are not necessarily unattended. This makes it important to consider
1594 whether manipulation of selective attention is adequate to render irrelevant stimuli truly
1595 unattended. For example, in a typical attention task where observers have to identify the central
1596 target while ignoring the distractors on the side (which can be compatible or incompatible with
1597 the target in terms of response), several steps should be considered to make attentional selection
1598 efficient (Lachter *et al.*, 2004; Miller, 1991; Yantis and Johnston, 1990):

- 1599
- 1600 1) The location where the target appears should be certain (e.g. a 100% valid pre-cue and a
1601 fixation marker of the target location will be helpful).
 - 1602 2) The location where the target appears, while always made clear to the observers such as
1603 through pre-cueing, may vary from trial to trial to reduce observers' tendency to explore new,
1604 unattended objects (Posner and Cohen, 1984).
 - 1605 3) Abrupt onsets of the target and distractors should be controlled because abrupt onsets can
1606 capture attention (Yantis and Jonides, 1984).
 - 1607 4) Grouping of the target and distractors (e.g. close proximity, common onset, and similar
1608 appearance) should be minimized because attention can be allocated to the entire grouped
1609 object (Duncan, 1984).
 - 1610 5) Duration of the distractors should be short (e.g. the distractors can be briefly presented and
1611 then masked) because observers tend to attend to the whole space of a scene if time allows and

1612 long duration will result in more unconsumed attentional capacity

1613 6) Perceptual load of target processing should be high enough to prevent involuntary spillover

1614 of unconsumed attentional capacity (Lavie, 1995).

1615 7) The target and distractors should be equally crowded (e.g. present stimuli in a circle), since

1616 stimuli at the beginning and end of an array are more salient than others (Flom *et al.*, 1963).

1617 8) Stimuli should be separated by more than 1° due to the limited resolution of attention.

1618 9) The target-response mapping may vary to prevent automatic mapping due to practice, which

1619 does not use attentional resources (Schneider and Shiffrin, 1977).

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1621 In particular, the load theory (Lavie, 1995, 2005), as described in item 6, specifies how capacity

1622 limitation determines the level of distractor processing, and serves as a powerful paradigm to

1623 render irrelevant stimuli as either unattended or involuntarily attended while keeping distractors

1624 constant across different conditions. The key tenet is that as long as the central task does not

1625 consume all or most of the available capacity, you cannot but process the distractors (e.g. Volker

1626 *et al.*, under review). Importantly, however, when steps like those listed above are considered to

1627 optimize selection efficiency, it is possible to render irrelevant stimuli unattended (as indexed

1628 by minimal processing of distractors) even under low perceptual load condition (Lachter *et al.*,

1629 2004).

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Figure Captions

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1634 *Figure 1.* Schematic of (a) binocular rivalry (BR) and (b) continuous flash suppression (CFS):

1635 two dissimilar images (panel “Stimulus”) are projected to each of two eyes through a mirror

1636 stereoscope (c); the left eye receives an image different from what the right eye receives. The

1637 two images compete with each other, resulting in alternative percepts during BR, or constant

1638 percept of random noise during CFS (panel “Percept”).

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1640 *Figure 2.* How contrast of adaptors modulates awareness-dependent adaptation. (a)

1641 Compressive nonlinearity of contrast-aftereffect function: aftereffect (AE) strength saturates at

1642 moderate to high contrast levels. (b) Rival stimuli used in threshold elevation AE and motion

1643 AE experiments. (c) Static motion AE duration in different viewing conditions at two adapting

1644 contrast levels (low vs. high). (d) Threshold elevation AE in different viewing conditions at two

1645 adapting contrast levels (low vs. high). Error bars indicate SEM. Adapted from Blake et al.,

1646 2006.

1647 *Figure 3.* Cortical responses to invisible tools and faces in the human dorsal and ventral

1648 pathways. (a) Continuous flash suppression paradigm: in the invisible condition, objects (or

1649 scrambled objects, serving as a baseline) were rendered invisible by dynamic, high-contrast,

1650 random textures presented to the dominant eye (shown); in the visible condition, high contrast

1651 dynamic noise was replaced by blank field (not shown). (b) Object-sensitive areas: V3A/V7,

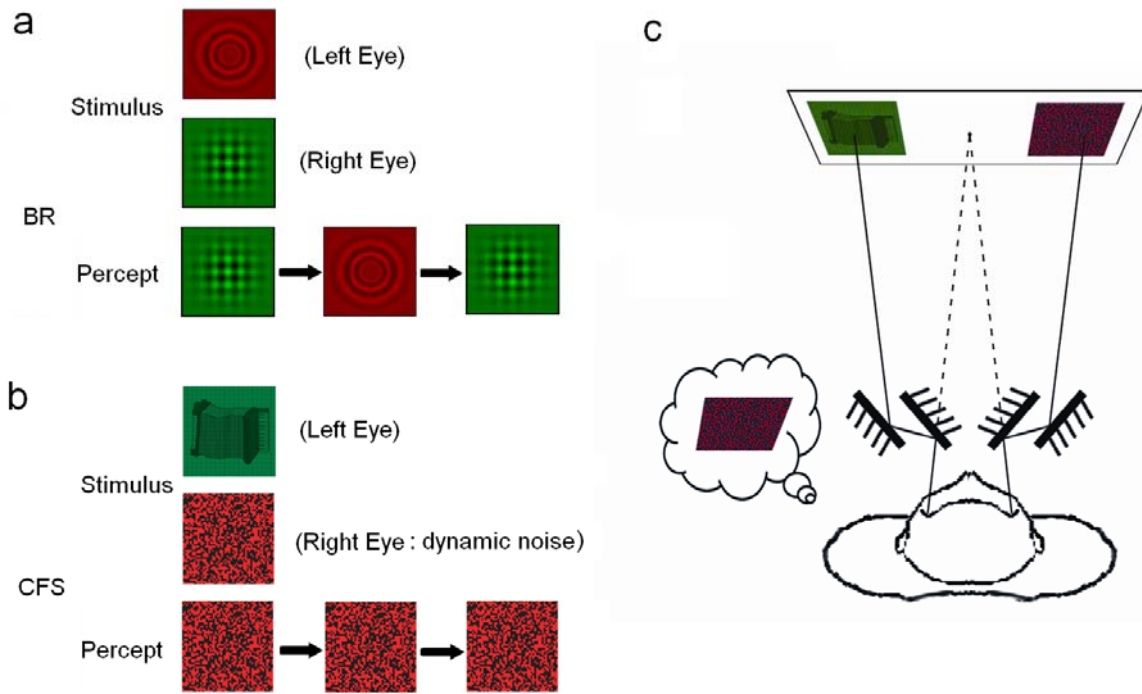
1652 intraparietal sulcus (IPS) in the dorsal pathway and the lateral occipital complex (LOC), temporal

1653 object areas in the ventral pathway. (c) Results for images of objects: Time courses of the average
1654 blood oxygen level dependent (BOLD) signals (percentage change) from dorsal and ventral
1655 object sensitive areas in 'visible' (gray curves) and 'invisible' (black curves) conditions. (d)
1656 Results for images of faces and tools: The average percentage change in BOLD signal from the
1657 dorsal object-sensitive areas in both the 'visible' and 'invisible' conditions. Error bars indicate
1658 SEM. Adapted from Fang and He, 2005.

1659 *Figure 4.* Attentional guidance by invisible erotic pictures. (a) Orientation task: participants were
1660 asked to indicate the perceived orientation (clockwise or counterclockwise) of a briefly presented
1661 Gabor patch. In the invisible condition, erotic pictures were rendered invisible by noise patches
1662 presented to the dominant eye (shown); in the visible condition, the noise patches was replaced
1663 by the same pair of intact and scrambled pictures (not shown). (b) Results for heterosexual male
1664 (Left) and heterosexual female (Right) observers: the attentional effect was defined by the
1665 accuracy difference between the erotic (i.e. when the Gabor patch was presented on the side of
1666 the erotic picture) and the scrambled (i.e. when the Gabor patch was presented on the side of the
1667 scrambled picture) conditions. Thus, a positive attentional effect suggested that attention was
1668 attracted to the erotic picture, whereas a negative attentional effect suggested that attention was
1669 repelled from the erotic picture. Same gender means that the gender of the picture is the same as
1670 the observers; whereas opposite gender means otherwise. * indicates $P < 0.05$; ** indicates $P <$
1671 0.0001 ; error bars indicate SEM. Adapted from Jiang et al., 2006.

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1673 Figure 1



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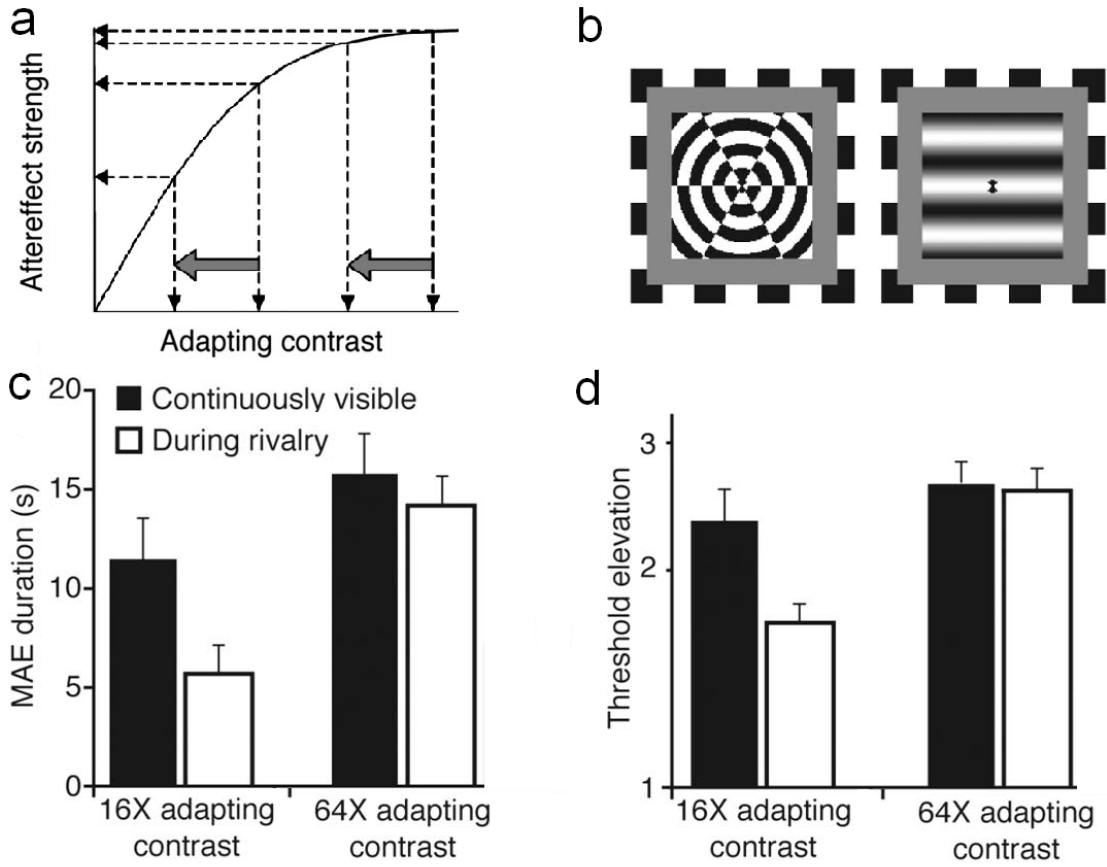
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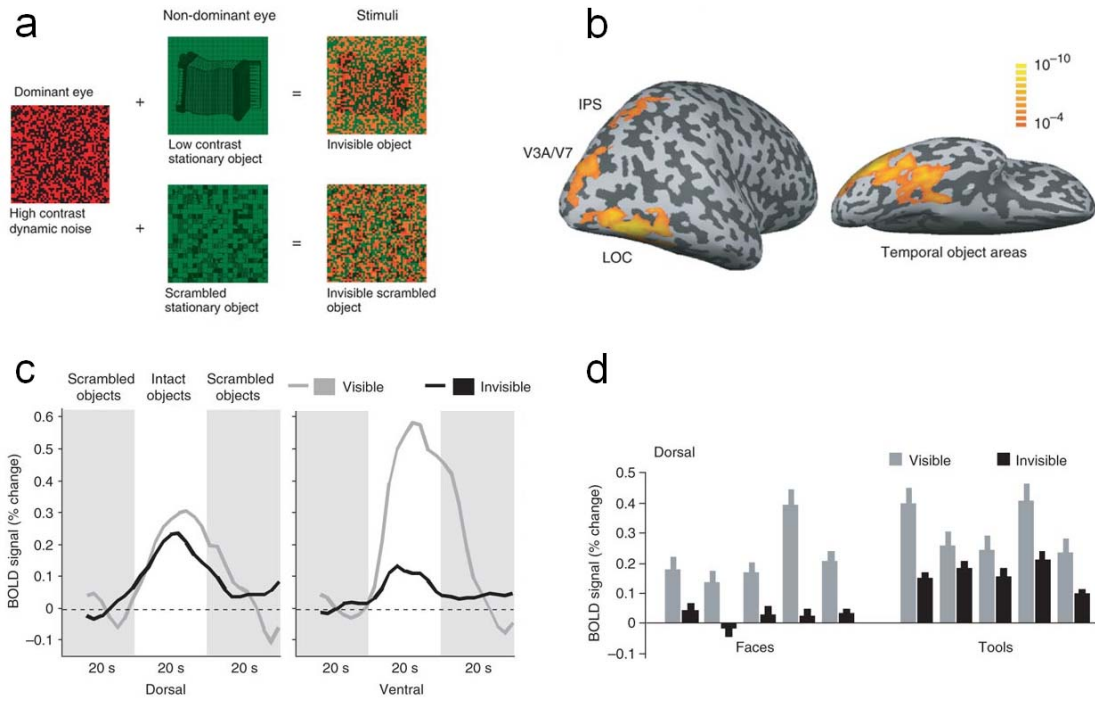
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1697 **Figure 3**



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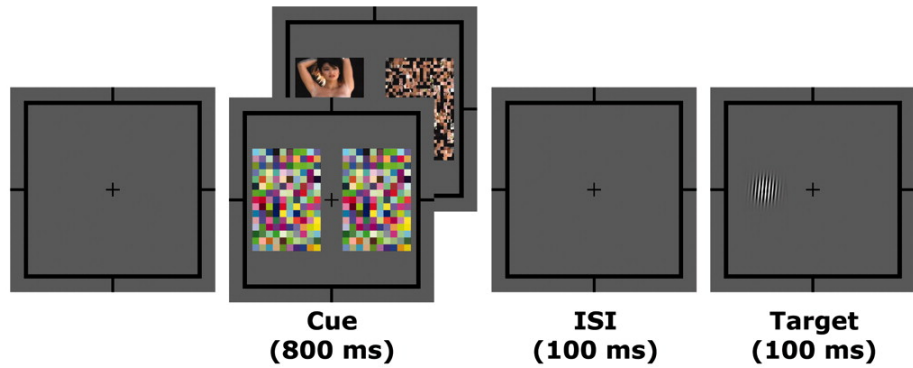
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