

# Attention and consciousness: two distinct brain processes

### Christof Koch<sup>1</sup> and Naotsugu Tsuchiya<sup>2</sup>

- <sup>1</sup> Division of Biology 216–76, California Institute of Technology, Pasadena, CA 91125, USA
- <sup>2</sup> Division of the Humanities and Social Sciences, 228–77, California Institute of Technology, Pasadena, CA 91125, USA

close relationship between attention consciousness has led many scholars to conflate these processes. This article summarizes psychophysical evidence, arguing that top-down attention and consciousness are distinct phenomena that need not occur together and that can be manipulated using distinct paradigms. Subjects can become conscious of an isolated object or the gist of a scene despite the near absence of top-down attention; conversely, subjects can attend to perceptually invisible objects. Furthermore, top-down attention and consciousness can have opposing effects. Such dissociations are easier to understand when the different functions of these two processes are considered. Untangling their tight relationship is necessary for the scientific elucidation of consciousness and its material substrate.

### Introduction

Commonly used in everyday speech and in the scholarly literature, 'attention' and 'consciousness' have resisted clear and compelling definition. As argued elsewhere [1,2], this unfortunate state of affairs will remain until the mechanistic basis of these phenomena has been enunciated thoroughly at the neuronal and molecular levels.

Few would dispute that the relationship between selective attention and consciousness is an intimate one. When we attend to an object, we become conscious of its attributes; when we shift attention away, the object fades from consciousness. This has prompted many to posit that these two processes are inextricably interwoven, if not identical [3-6]. Others, however, going back to the 19th century [7], have argued that attention and consciousness are distinct phenomena that have distinct functions and neuronal mechanisms [2,8–17]. If this proposition were true, what would be the nature of their causal interaction? Is paying attention necessary and sufficient for consciousness? Or can conscious perception occur outside the spotlight of attention? Of course, this presupposes that consciousness is a unitary concept, which is not the case; consciousness has been dissected on conceptual grounds (access versus phenomenal consciousness), ontological grounds (hard problem versus easy problem) and psychological grounds (explicit versus implicit processes).

Here, we summarize recent psychophysical evidence in support of a dissociation between attention and consciousness, and provide functional justifications for this viewpoint. We argue that events or objects can be attended to without being consciously perceived. Furthermore, an event or object can be consciously perceived in the near absence of top-down attentional processing. Note that our usage of 'attention' always implies selective attention, rather than the processes that control the overall level of arousal and alertness.

### Functional roles of attention and consciousness

Complex organisms and brains can suffer from informational overload. In primates, about one million fibers leave each eye, carrying on the order of one megabyte per second of raw information. One way to deal with this deluge is to select a small fraction and process this reduced input in real time, while the non-attended portion of the input is processed at a reduced bandwidth. In this view, attention 'selects' information of current relevance to the organism, while the non-attended data are neglected.

Since the time of Williams James, it has been known that selection is based on either bottom-up exogenous or top-down endogenous factors. Exogenous cues are imageimmanent features that transiently attract attention or eye gaze, independent of a particular task. Thus, if an object attribute (e.g. flicker, motion, color, orientation, depth or texture) differs significantly from a neighboring attribute, the object will be salient. This definition of bottom-up saliency has been implemented into a suite of neuromorphic vision algorithms that have at their core a topographic saliency map that encodes the saliency or conspicuity of locations in the visual field, independent of the task [18]. [See iLab Neuromorphic Vision C++ Toolkit (http://iLab.usc.edu) for a C++ implementation, and Saliency Toolbox (http://www.saliencytoolbox.net) for a Matlab toolbox.] Such algorithms account for a significant proportion of scanning eye movements [19,20].

However, under many conditions, subjects disregard salient, bottom-up cues when searching for particular objects in a scene, by dint of top-down, task-dependent control of attention. Bringing top-down, sustained attention to bear on an object or event in a scene takes time. Top-down attention selects input defined by a circumscribed region in space (focal attention), by a particular feature (feature-based attention) or by an object (object-based attention). It is on the relationship between these volitionally controlled forms of selective, endogenous attention and consciousness that this article focuses.

Consciousness is surmised to have substantially different functions from attention. These include summarizing all information that pertains to the current state of the organism and its environment and ensuring this compact summary is accessible to the planning areas of the brain, and also detecting anomalies and errors, decision making, language, inferring the internal state of other animals, setting long-term goals, making recursive models and rational thought.

To the extent that one accepts that attention and consciousness have different functions, one must also accept that they cannot be the same process. It follows, then, that any conscious or unconscious percept or behavior can be classified in one of four ways, depending on whether top-down attention is required and whether it necessarily gives rise to consciousness.

## The four ways of processing visual events and behaviors

Although many scholars agree that attention and consciousness are distinct, they insist that attention is necessary for consciousness, and that non-attended events remain hidden. For example, Dehaene *et al.* [16] state that considerable evidence indicates that, without attention, conscious perception cannot occur. We now review evidence that argues otherwise.

### Attention with consciousness

When we attend to a face or to an object within a cluttered scene, we usually become conscious of its attributes and have access to all of the attendant privileges of consciousness (e.g. working memory and verbal reportability). Although the minimal neuronal mechanisms that are jointly sufficient for any one conscious percept remain elusive, evidence from models agrees that these mechanisms must involve a reciprocal relationship between cellular populations in extrastriate visual cortices and neurons in the premotor and prefrontal cortices, mediated by long-range corticocortical feedforward and feedback projections [1,14,21–23].

More than a century of research has quantified the ample benefits afforded by attention and conscious perception. For example, Mack and Rock [24] demonstrated compellingly that subjects must attend to novel or unexpected stimuli to become conscious of them. These percepts occupy the lower-right quadrant of our attention—consciousness design matrix (Table 1).

### No attention, no consciousness

At the other end of the spectrum are objects or events that do not benefit from a top-down attentional bias. Under these conditions, the associated net wave of spiking activity moving from the retina into primary visual cortex and beyond will not trigger a conscious percept (see 'Processing without top-down attention and consciousness'). However, such non-attended or minimally attended, non-conscious activity can still be causally effective and leave traces that can be detected using sensitive behavioral techniques. For instance, we surmise that negative afterimages [25–27] can be produced by invisible stimuli in the (near) absence of top-down attention. These occupy the upper-left quadrant of Table 1.

What about the two remaining quadrants, which cover events and behaviors that require top-down attention but do not give rise to conscious perception, and events and behaviors that give rise to consciousness without top-down attention? These can be studied using techniques that independently manipulate top-down attention and visual consciousness (Box 1).

### Attention without consciousness

Subjects can attend to a location for many seconds and yet fail to see one or more attributes of an object at that location (lower-left quadrant in Table 1). In lateral masking (visual crowding), the orientation of a peripherally presented grating is hidden from conscious sight but remains sufficiently potent to induce an orientationdependent aftereffect [28]. An aftereffect induced by an invisible illusory contour can require focal attention even when the object at the center of attention is invisible [29]. Furthermore, priming has been elicited [10] for invisible words (suppressed by a combination of forward and backward masking), but only if the subject was attending to the invisible prime-target pair; without attention, the same word fails to elicit priming. Male and female nudes attract attention when they are rendered completely invisible by continuous flash suppression [30]. Interestingly, in heterosexuals, these effects are apparent only for nudes of the opposite sex. Note that without the mask, these stimuli are clearly visible. Likewise, the blindsight patient GY has the usual reaction-time advantages for the detection of targets in his blind visual field when attentionally cued, even when the cues are located in his blind field [13] (see also Refs [31,32] for further evidence).

Table 1. A fourfold classification of conscious and unconscious percepts and behaviors<sup>a</sup>

	Might not give rise to consciousness	Gives rise to consciousness
Top-down attention is not required	Formation of afterimages	Pop-out in search
	Rapid vision (<120 ms)	Iconic memory
	Zombie behaviors	Gist
		Animal and gender detection in dual tasks
		Partial reportability
Top-down attention is required	Priming	Working memory
	Adaptation	Detection and discrimination of unexpected and
	Visual search	unfamiliar stimuli
	Thoughts	Full reportability

<sup>&</sup>lt;sup>a</sup>This classification organizes conscious and unconscious percepts and behaviors into four, psychophysically defined, categories, depending on whether top-down attention is necessary and whether they necessarily give rise to phenomenal consciousness.

### Box 1. Psychophysical methods for independent manipulation of visual consciousness and top-down attention

Top-down attention and consciousness can be tightly coupled. To dissociate them, experimental methods are required that manipulate either attention or consciousness, independently or semi-independently, in a specific manner with few side effects. The dual-tasks paradigm [36,37] manipulates top-down, focal attention without affecting bottom-up saliency; a central, attentional-demanding discrimination task is presented at the center of gaze, while a secondary stimuli is projected in the periphery (Figure la of this box). Subjects carry out either the central task or the peripheral task, or both simultaneously, while the scene and its layout remain the same. Surprisingly, seemingly complex peripheral tasks can be performed equally well under either the single-task or dual-tasks condition [38–40], whereas computationally simpler tasks deteriorate when performed simultaneously with the

central task (Figure lb,c). The dual-tasks paradigm quantifies what type of stimulus attributes can be signaled and consciously perceived in the near absence of top-down spatial attention [51].

Visual consciousness is manipulated using a multitude of techniques, such as backward masking, standing wave of invisibility, crowding, bistable figures (Figure Id), binocular rivalry, flash suppression, continuous flash suppression [26,52], motion-induced blindness and attentional blink (for a review, see Ref. [53]). These techniques control the visibility of an object or part of an object in space and time. The dual-tasks paradigm can be combined with these methods, enabling the independent manipulation of top-down attention and consciousness (Figure Ie), although we await a full factorial analysis for many popular experiments (Box 2).

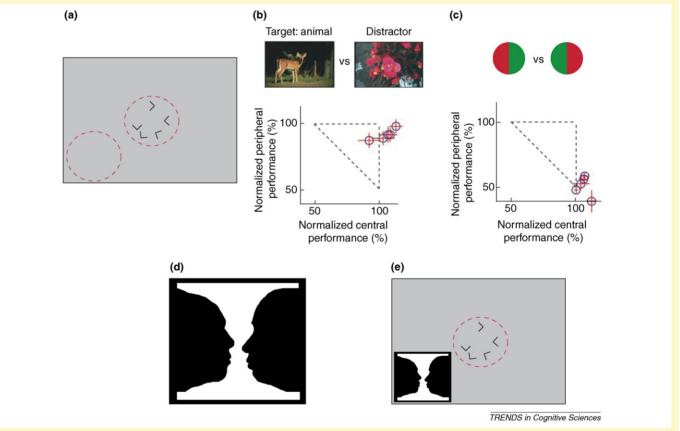


Figure I. The dual-tasks paradigm. (a) The dual-tasks paradigm studies how performance of a secondary task in the periphery (empty red circle) is affected when a centrally presented attention-demanding task (centered red circle) is performed simultaneously. (b) Participants can decide whether a natural scene includes an animal at the same time as performing a central task. Scene categorization task performance (y-axis) remains at the same level under single-task (normalized to 100% on the y-axis) and dual-tasks (depicted as circles with standard error of the mean) conditions. Note that the central task performance (x-axis) also remains the same in single-task (normalized to 100% on the x-axis) and dual-tasks (shown as circles) situations. (c) However, participants are unable to distinguish between a red–green disk and a green-red one when attention is engaged at the center. (d) An example of a bistable conscious percept (Rubin's vase: two silhouettes versus a vase). (e) The effect of withdrawing top-down attention could be characterized by embedding Rubin's vase, a bistable percept, into a dual-tasks experiment [54] (Box 2). Figure lb,c modified from Ref. [38].

Finally, feature-based attention can spread to invisible stimuli [33,34]. Indeed, when searching for an object in a cluttered scene (e.g. keys in a messy room), attention is paid to an invisible object and its associated features. This research shows that attentional selection does not necessarily engender conscious sensation.

Consciousness in the near absence of attention Conversely, when focusing intensely on one event, the world is not perceived as a tunnel, with everything outside the focus of attention gone (upper-right quadrant in Table 1). We are always aware of some aspects of the world that surrounds us, such as its gist. Indeed, gist is immune from inattentional blindness [24]: when a photograph was briefly flashed unexpectedly onto a screen, subjects could accurately report a summary of the photograph. In a mere 30 ms presentation time, the gist of a scene can be apprehended. This is insufficient time for top-down attention to play much of a role. Furthermore, because gist is a property associated with the entire image, any process that locally enhances features, such as focal attention, will be of limited use.

A common arrangement in many experiments involves studying the perception of a single object (e.g. a bar) in an otherwise empty display. In this situation, what function would top-down, selective attention need to perform when there is no competing object in or around fixation? Indeed, the most popular neuronal model of attention, biased competition [35], predicts that in the absence of competition, no or little attentional enhancement occurs (see also Ref. [12]).

In a dual-tasks paradigm, the subject's attention is drawn to an attentionally demanding central task, while at the same time a secondary stimulus is flashed in the periphery [36,37] (Box 1). With focal attention busy at the center, subjects can determine whether a scene contains an animal (or a vehicle) but are unable to distinguish between a red-green and a green-red disk [38]. Likewise, subjects can distinguish between male and female faces in the periphery or even between famous and non-famous faces [39,40]. However, remarkably, subjects are frustrated by tasks that are computationally much simpler (e.g. discriminating between a rotated 'L' and a rotated 'T'). Thus, although it cannot be said with certainty that observers do not deploy some top-down attention to the peripheral target in dual-tasks experiments that require training and concentration (i.e. high arousal), it seems that subjects can perform certain discriminations in the near absence of top-down attention. And they are not guessing: they can be confident of their discrimination choices and 'see', albeit often indistinctly, the peripheral stimuli.

# Processing without top-down attention and consciousness

Visual input can be classified rapidly. As demonstrated by Kirchner and Thorpe [41], at  $\sim$ 120 ms, the brain can begin to determine whether a briefly flashed image contains animals or not. At this speed, it is no surprise that subjects often respond without having consciously seen the image; consciousness of the image might come later or not at all. Dual-tasks and dual-presentation paradigms support the idea that such discriminations can occur in the near absence of focal, spatial attention [38,42], implying that purely feedforward networks can support complex visual decision making [43,44]. Supporting this conclusion are neurophysiologically grounded computer models of the feedforward stages of the visual-processing hierarchy [45] that achieve human-like performance levels in such categorization tasks (T. Serre et al., unpublished; see http://cbcl.mit.edu/publications/ ps/SerreOlivaPoggio06.pdf).

Animal experiments could prove this assertion. Imagine that all the corticocortical pathways from prefrontal cortex back to visual cortex could be transiently knocked out using a molecular silencing tool (without compromising feedforward processing). That is, for a couple of hours, the brain of a monkey would support only feedforward pathways. It is likely that such an animal could still perform a previously learnt rapid discrimination task with the same level of performance as before the intervention (upper-left quadrant in Table 1), without top-down attention and without conscious perception.

### Attention and consciousness can oppose each other

Withdrawing top-down attention from a stimulus and cloaking it from consciousness can have opposing effects. When observers try to find two embedded targets within a rapidly flashed stream of images, they often fail to see the second target, the attentional blink [46]. Counterintuitively, Olivers and Nieuwenhuis [47] found that observers can see both the first and the second targets better when they are distracted by a simultaneous auditory dual task or when they are encouraged to think about task-irrelevant events. Recent work on afterimages, stabilization of bistable figures and complex decision making hint at striking dissociations between the effects of manipulating attention and consciousness independently (Box 2). Such findings are difficult to understand within a framework that aligns top-down attention closely with consciousness.

#### Relationship to other conceptual distinctions

Dehaene and colleagues [16] propose a tripartite ontology, based on the global workspace hypothesis of Baars (for an updated view, see Ref. [14]) and Dehaene et al. [23], whereby any physical stimulus triggers subliminal, preconscious or conscious processing. What decides the fate of a stimulus is its strength and whether or not top-down attention is deployed. This threefold distinction maps onto our fourfold one if subliminal processing is equated with the two left quadrants and preconscious processing with the upper-right quadrant (Table 1). One important difference is our assumption that consciousness can occur without top-down attention (upper-right quadrant). A priori, there is no fundamental reason why global workspace theory requires actively paying attention to a stimulus in order to be conscious of it. There might be many routes by which the global workspace could be accessed, in addition to that of top-down attention.

### Do these conclusions hold for real life?

It could be contested that top-down attention without consciousness and consciousness with little or no top-down attention are arcane laboratory curiosities that have little relevance to the real world. We believe otherwise. A lasting insight into human behavior – eloquently articulated by Friedrich Nietzsche – is that much action bypasses conscious perception and introspection. In particular, Goodale and Milner [48] isolated highly trained, automatic, stereotyped and fluid visuomotor behaviors that work in the absence of phenomenal experience. As anybody who runs mountain trails, climbs, plays soccer or drives home on automatic pilot knows, these sensorimotor skills – dubbed zombie behaviors [49] - require rapid and sophisticated sensory processing. Confirming a long-held belief among trainers, athletes perform better at their highly tuned skill when they are distracted by a skill-irrelevant dual task (e.g. paying attention to tones) than when they pay attention to their exhaustively trained behaviors [50].

The history of any scientific concept (e.g. energy, atoms or genes) is one of increasing differentiation and sophistication until its action can be explained in a quantitative and mechanistic manner at a lower, more elemental level. We are far from this ideal in the inchoate science of consciousness. Yet functional considerations and the

20

### Attention and its neuronal correlate can be understood in the context of selection and biased competition [35]; attention acts as a winnertakes-all, enhancing one coalition of neurons (representing the

attended object) at the expense of others (non-attended stimuli). Paradoxically, reducing attention can enhance awareness [47] and certain behaviors [50].

Consider the formation of afterimages (Figure Ia of this box). If an item is attended to during adaptation, the intensity of the subsequent afterimage becomes weaker and its duration shorter compared with an unattended item [55,56] (Figure Ib). However, if the image is perceptually suppressed during adaptation, the afterimage is substantially weakened [26,27]. Thus, focal attention and consciousness have opposing effects.

Next, consider freezing in bistable perception [57] (Figure Ic). During continuous viewing of an ambiguous stimulus, the percept flips stochastically. Yet if the bistable figure is briefly removed (leaving the display empty), the dominant percept at the start of the new display is the same as when the percept disappeared. This freezing is disrupted if spatial attention is distracted from the empty display [58], most probably by disrupting memory buildup. This can be thought of as speeding up perceptual switching. Yet distracting focal attention during bistable perception slows down the switching

rate [54] (Figure Id). In other words, withdrawing focal attention when the stimulus is invisible (i.e. not consciously seen) disrupts perceptual freezing, whereas withdrawing attention when the stimulus is visible slows down switching.

Finally, consider complex decision making (Figure le). The study by Dijksterhuis et al. [59] consisted of three phases: examination of items, deliberation and decision. Either four or 12 properties for each of four cars were shown one at a time during the examination phase. Subjects then deliberated for several minutes without the attributes being visible (i.e. subjects had to remember them; this can be thought of as an 'invisible' condition) before making a purchasing decision. Dijksterhuis et al. manipulated whether or not subjects were kept busy by performing a cognitively engaging task during the deliberation period. They concluded that when faced with working-memory overload, an explicit strategy based on deliberate and rational thought leads to poor decision making, whereas distracting subjects while they decide which car to buy greatly increases the probability of a good decision (Figure If). We surmise that if the list of items were present throughout the decision-making period, thereby reducing working-memory load, an attention-distracting task would degrade purchasing performance. Note that a complete independent manipulation of attention and consciousness has not been performed in any of these examples.

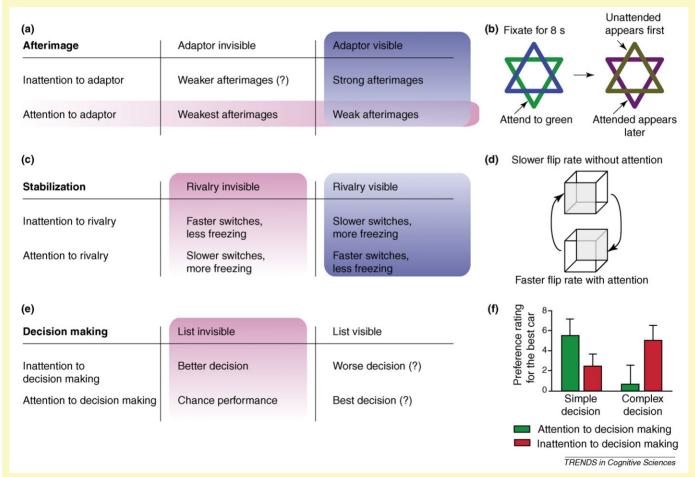


Figure I. Three examples of dissociation of the effects of attention and awareness. (a,b) When an adaptor is attended to, the associated afterimage becomes weaker and appears later (blue gradation) [55,56]; note that the afterimages are fainter than graphically indicated. Yet, paradoxically, when the adaptor is rendered invisible, its afterimage is substantially weakened (pink gradation) [26,27]. (c,d) When attention is withdrawn from a visible bistable rivalry target (e.g. a Necker cube), the rate of perceptual flips slows down (blue gradation) [54]. When the target stimulus is intermittently presented (stabilization), the opposite occurs: withdrawing attention from the target causes less stabilization and the perceptual flip rate speeds up (pink gradation) [58]. (e,f) When confronted with a complex decision for which many items must be remembered (i.e. the list is invisible), distracting subjects from the decision-making process improves performance (pink gradation) [59]. '(?)' indicates that data are not available at this point. Figure If modified from Ref. [59].

#### Box 3. Questions for future research

- When studying the neuronal correlates of consciousness (NCC), great care must be taken to untangle the effects of top-down attention from those of consciousness [60–62]. Have the suggested NCC been confounded by attentional effects?
- Does perception of gist, a high-level semantic description of a scene (e.g. two people drinking; a man walking a dog), depend on focal, top-down attention? How good are people at describing the gist of novel, natural scenes under dual-tasks conditions?
- What are the neuronal mechanisms that lead to improved zombie behaviors in the near absence of top-down attention [50]? Do those aspects of reasoning, language processing and thinking that proceed in the absence of consciousness function better without top-down attention?
- The arguments outlined in this article also apply for other modalities (i.e. hearing and touch), although it might be difficult to find ways to manipulate awareness of stimuli. Can robust illusions be found to manipulate awareness in other modalities?
  Can attention be shown without awareness and awareness be shown without attention, and what are the opposing effects of the two in these modalities?

empirical and conceptual work of many scholars over the past decade make it clear that these psychologically defined processes – top-down attention and consciousness – so often conflated, are not the same. This empirical and functional distinction clears the deck for a concerted neurobiological attack on the core problem – that of identifying the necessary and sufficient neural causes of a conscious percept (see Box 3 for Questions for future research).

### Acknowledgements

Owing to space limitations, we could not discuss all the relevant literature and apologize to those whose work was not cited here. We thank R. Blake, N. Block, A. Cleeremans, S. He, Y. Jiang, R. Kanai, V. Lamme, C. Paffen, and M. Snodgrass for discussion. We thank the participants of our tutorial at ASSC10 Oxford for their feedback. This research was supported by the NIMH, the NSF, the Keck Foundation, the Moore Foundation, and the Tom Slick Research Awards from the Mind Science Foundation.

### References

- 1 Crick, F. and Koch, C. (2003) A framework for consciousness. Nat. Neurosci. 6, 119–126
- 2 Koch, C. (2004) The Quest for Consciousness: a Neurobiological Approach, Roberts and Publishers
- 3 O'Regan, J.K. and Noe, A. (2001) A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24, 939–973
- 4 Posner, M.I. (1994) Attention: the mechanisms of consciousness. *Proc. Natl. Acad. Sci. U. S. A.* 91, 7398–7403
- 5 Velmans, M. (1996) The Science of Consciousness, Routledge
- 6 Merikle, P.M. and Joordens, S. (1997) Parallels between perception without attention and perception without awareness. *Conscious. Cogn.* 6, 219–236
- 7 Wundt, W. (1874) Grundzüge der physiologischen Psychologie, Engelmann
- 8 Iwasaki, S. (1993) Spatial attention and two modes of visual consciousness. *Cognition* 49, 211–233
- 9 Hardcastle, V.G. (1997) Attention versus consciousness: a distinction with a difference. Cognitive Studies. Bulletin of the Japanese Cognitive Science Society 4, 56–66
- 10 Naccache, L. et al. (2002) Unconscious masked priming depends on temporal attention. Psychol. Sci. 13, 416–424
- 11 Lamme, V.A. (2003) Why visual attention and awareness are different. Trends Cogn. Sci. 7, 12–18
- 12 Woodman, G.F. and Luck, S.J. (2003) Dissociations among attention, perception, and awareness during object-substitution masking. *Psychol. Sci.* 14, 605–611

- 13 Kentridge, R.W. et al. (2004) Spatial attention speeds discrimination without awareness in blindsight. Neuropsychologia 42, 831–835
- 14 Baars, B.J. (2005) Global workspace theory of consciousness: toward a cognitive neuroscience of human experience. *Prog. Brain Res.* 150, 45– 53
- 15 Block, N. (2005) Two neural correlates of consciousness. Trends Cogn. Sci. 9, 46–52
- 16 Dehaene, S. et al. (2006) Conscious, preconscious, and subliminal processing: a testable taxonomy. Trends Cogn. Sci. 10, 204–211
- 17 Bachman, T. (2006) A single metatheoretical framework for a number of conscious-vision phenomena. In *Psychological Science Around the World* (Jing, Q., ed.), pp. 229–242, Psychology Press
- 18 Itti, L. and Koch, C. (2001) Computational modelling of visual attention. Nat. Rev. Neurosci. 2, 194–203
- 19 Parkhurst, D. et al. (2002) Modeling the role of salience in the allocation of overt visual attention. Vision Res. 42, 107–123
- 20 Peters, R.J. et al. (2005) Components of bottom-up gaze allocation in natural images. Vision Res. 45, 2397–2416
- 21 Tononi, G. and Edelman, G.M. (1998) Consciousness and complexity. Science 282, 1846–1851
- 22 Lamme, V.A. and Roelfsema, P.R. (2000) The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* 23, 571–579
- 23 Dehaene, S. et al. (2003) A neuronal network model linking subjective reports and objective physiological data during conscious perception. Proc. Natl. Acad. Sci. U. S. A. 100, 8520–8525
- 24 Mack, A. and Rock, I. (1998) Inattentional Blindness, MIT Press
- 25 Hofstoetter, C. et al. (2004) Motion-induced blindness does not affect the formation of negative afterimages. Conscious. Cogn. 13, 691–708
- 26 Tsuchiya, N. and Koch, C. (2005) Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101
- 27 Gilroy, L.A. and Blake, R. (2005) The interaction between binocular rivalry and negative afterimages. Curr. Biol. 15, 1740–1744
- 28 He, S. et al. (1996) Attentional resolution and the locus of visual awareness. Nature 383, 334–337
- 29 Montaser-Kouhsari, L. and Rajimehr, R. (2004) Attentional modulation of adaptation to illusory lines. J. Vis. 4, 434–444
- 30 Jiang, Y. et al. (2006) A gender- and sexual orientation-dependent spatial attentional effect of invisible images. Proc. Natl. Acad. Sci. U.S.A., DOI: 10.1073/pnas.0605678103 (http://www.pnas.org)
- 31 Rajimehr, R. (2004) Unconscious orientation processing. Neuron 41,  $663{-}673$
- 32 Sumner, P. et al. (2006) Attentional modulation of sensorimotor processes in the absence of perceptual awareness. Proc. Natl. Acad. Sci. U. S. A. 103, 10520–10525
- 33 Melcher, D. et al. (2005) Implicit attentional selection of bound visual features. Neuron 46, 723–729
- 34 Kanai, R. et al. The scope and limits of top-down attention in unconscious visual processing. Curr. Biol. (in press)
- 35 Desimone, R. and Duncan, J. (1995) Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18, 193–222
- 36 Sperling, G. and Dosher, B. (1986) Strategy and optimization in human information processing. In *Handbook of Perception and Human Performance* (Boff, K.R. et al., eds), pp. 1–65, Wiley
- 37 Braun, J. and Julesz, B. (1998) Withdrawing attention at little or no cost: detection and discrimination tasks. Percept. Psychophys. 60, 1–23
- 38 Li, F.F. et al. (2002) Rapid natural scene categorization in the near absence of attention. Proc. Natl. Acad. Sci. U. S. A. 99, 9596–9601
- 39 Reddy, L. et al. (2006) Face identification in the near-absence of focal attention. Vision Res. 46, 2336–2343
- 40 Reddy, L. et al. (2004) Face-gender discrimination is possible in the near-absence of attention. J. Vis. 4, 106–117
- 41 Kirchner, H. and Thorpe, S.J. (2006) Ultra-rapid object detection with saccadic eye movements: visual processing speed revisited. *Vision Res.* 46, 1762–1776
- 42 Rousselet, G.A. et al. (2002) Parallel processing in high-level categorization of natural images. Nat. Neurosci. 5, 629–630
- 43 VanRullen, R. et al. (2001) Feed-forward contour integration in primary visual cortex based on asynchronous spike propagation. Neurocomputing 38, 1003–1009
- 44 VanRullen, R. and Koch, C. (2003) Visual selective behavior can be triggered by a feed-forward process. J. Cogn. Neurosci. 15, 209– 217

22

- 46 Raymond, J.E. et al. (1992) Temporary suppression of visual processing in an RSVP task: an attentional blink? J. Exp. Psychol. Hum. Percept. Perform, 18, 849-860
- 47 Olivers, C.N. and Nieuwenhuis, S. (2005) The beneficial effect of concurrent task-irrelevant mental activity on temporal attention. Psychol. Sci. 16, 265-269
- 48 Goodale, M.A. and Milner, D.A. (2004) Sight Unseen: an Exploration of Conscious and Unconscious Vision, Oxford University Press
- 49 Koch, C. and Crick, F. (2001) The zombie within. Nature 411, 893
- 50 Beilock, S.L. et al. (2002) When paying attention becomes counterproductive: impact of divided versus skill-focused attention on novice and experienced performance of sensorimotor skills. J. Exp. Psychol. Appl. 8, 6-16
- 51 VanRullen, R. et al. (2004) Visual search and dual tasks reveal two distinct attentional resources. J. Cogn. Neurosci. 16, 4-14
- 52 Tsuchiya, N. et al. (2006) Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. J. Vis. 6, 1068-1078
- 53 Kim, C.Y. and Blake, R. (2005) Psychophysical magic: rendering the visible 'invisible'. Trends Cogn. Sci. 9, 381-388

- 54 Paffen, C.L. et al. (2006) Attention speeds binocular rivalry. Psychol. Sci. 17, 752-756
- 55 Lou, L. (2001) Effects of voluntary attention on structured afterimages. Perception 30, 1439–1448
- 56 Suzuki, S. and Grabowecky, M. (2003) Attention during adaptation weakens negative afterimages. J. Exp. Psychol. Hum. Percept. Perform. 29. 793-807
- 57 Leopold, D.A. et al. (2002) Stable perception of visually ambiguous patterns. Nat. Neurosci. 5, 605-609
- 58 Kanai, R. and Verstraten, F.A. (2006) Attentional modulation of perceptual stabilization. Proc. Biol. Sci. 273, 1217-1222
- 59 Dijksterhuis, A. et al. (2006) On making the right choice: the deliberation-without-attention effect. Science 311, 1005-1007
- 60 Huk. A.C. et al. (2001) Neuronal basis of the motion aftereffect reconsidered. Neuron 32, 161-172
- 61 Tse, P.U. et al. (2005) Visibility, visual awareness, and visual masking of simple unattended targets are confined to areas in the occipital cortex beyond human V1/V2. Proc. Natl. Acad. Sci. U. S. A. 102, 17178-
- 62 Moradi, F. et al. Activity in visual cortex is modulated by top-down attention locked to reaction time. J. Cogn. Neurosci. (in press)

### Five things you might not know about Elsevier

1.

Elsevier is a founder member of the WHO's HINARI and AGORA initiatives, which enable the world's poorest countries to gain free access to scientific literature. More than 1000 journals, including the Trends and Current Opinion collections and Drug Discovery Today, are now available free of charge or at significantly reduced prices.

The online archive of Elsevier's premier Cell Press journal collection became freely available in January 2005. Free access to the recent archive, including Cell, Neuron, Immunity and Current Biology, is available on ScienceDirect and the Cell Press journal sites 12 months after articles are first published.

3.

Have you contributed to an Elsevier journal, book or series? Did you know that all our authors are entitled to a 30% discount on books and stand-alone CDs when ordered directly from us? For more information, call our sales offices:

+1 800 782 4927 (USA) or +1 800 460 3110 (Canada, South and Central America) or +44 (0)1865 474 010 (all other countries)

Elsevier has a long tradition of liberal copyright policies and for many years has permitted both the posting of preprints on public servers and the posting of final articles on internal servers. Now, Elsevier has extended its author posting policy to allow authors to post the final text version of their articles free of charge on their personal websites and institutional repositories or websites.

The Elsevier Foundation is a knowledge-centered foundation that makes grants and contributions throughout the world. A reflection of our culturally rich global organization, the Foundation has, for example, funded the setting up of a video library to educate for children in Philadelphia, provided storybooks to children in Cape Town, sponsored the creation of the Stanley L. Robbins Visiting Professorship at Brigham and Women's Hospital, and given funding to the 3rd International Conference on Children's Health and the Environment.