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The Relationship Between Consciousness and Top-Down Attention

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INTRODUCTION

Commonly used in both everyday speech and scholarly literature, the terms “attention” and “consciousness” have resisted clear and compelling definitions. As argued elsewhere (Crick and Koch, 2003; Koch, 2004) this unfortunate state of affairs will probably remain until the mechanistic basis of these phenomena has been thoroughly enunciated.

Few would dispute that the relationship between selective attention and perceptual consciousness is an intimate one. When we pay attention to an object, we usually become conscious of its various 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 (O’Regan and Noe, 2001; Posner, 1994, 2012; Merikle and Joordens, 1997; Jackendoff, 1996; Prinz, 2004; Chun and Wolfe, 2000; Mole, 2008; Marchetti, 2012; De Brigard and Prinz, 2010; Cohen and Dennett, 2011). Others, going back to the nineteenth century (Wundt, 1874), however, have argued that attention and consciousness are distinct phenomena, with distinct functions and neuronal mechanisms (Iwasaki, 1993; Hardcastle, 1997; Naccache et al., 2002; Lamme, 2003; Woodman and Luck, 2003; Kentridge et al., 2004; Koch, 2004; Baars, 2005; Block,

2005; Dehaene et al., 2006; Bachmann, 2006; Koch and Tsuchiya, 2007; van Boxtel et al., 2010a; Lamme, 2010).

Even if the latter proposition is true, what is the nature of their causal interaction? Can we pay attention to an object or aspect of an object that is not consciously perceived? Is paying attention necessary for consciousness (Dehaene et al., 2006; Cohen et al., 2012), or can conscious perception occur outside the spotlight of attention?

We here summarize recent psychophysical, neuroimaging, and neurophysiological evidence in favor of a dissociation between selective attention and consciousness, and provide functional justifications for this reasoning. 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 amplification of neural signals. We review some remarkable evidence that top-down attention and consciousness can have opposing effects. We also refer to neuroimaging studies that measured attentional modulation of fMRI responses to invisible stimuli and that dissociated the effects of attention and consciousness by independently manipulating the visibility of and top-down attention to the stimuli. Finally, we speculate on the neuronal substrate of consciousness without top-down attention and discuss optogenetic studies in mice that promise to test the very idea of conscious perception without any top-down attention.

Note that our usage of “attention” always implies selective attention, rather than the processes that control the overall level of arousal and alertness. Furthermore, we restrict this review to visual attention and visual consciousness, as visual perception and the neurophysiology of vision is much better understood than that of other sensory modalities. For other modalities, see several articles featured in Tsuchiya and van Boxtel (2013).

Our usage of “consciousness” is not restricted to “visual consciousness” but, *mutatis mutandis*, applies to all forms of consciousness, whether perceptual or not. Indeed, we consider self-consciousness, highly developed in adult humans, to be a subclass of conscious experiences. Likewise, the feeling of freely willing an action, such as raising one’s arm, sometimes also referred to as *agency* (Fried et al., 1991; Wegner, 2002), is another subclass of conscious experience. While these experiences differ from the experiences associated with feeling pain or seeing red, common to all is subjectivity, is phenomenology. The question that this chapter addresses is the extent to which this feeling depends on selective attention.

FUNCTIONAL CONSIDERATIONS

Let us start by considering the functional roles of visual attention (Carrasco, 2011). Complex organisms, such as brains, suffer from informational overload. In

primates, about one million fibers leave each eye and carry on the order of one megabyte per second of raw information. One way to deal with this deluge of data 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 suffer from benign neglect.

At the neuronal level, attentional selection is implemented in at least three ways (Kastner and Ungerleider, 2000); (i) it increases the baseline neuronal activity (but also see Otazu et al., 2009); (ii) it amplifies the neuronal response to the selected location, feature, and object; this may occur by reducing noise correlations among neighboring neurons (Cohen and Maunsell, 2009; Mitchell et al., 2009) or by inactivating sub-types of different inhibitory interneurons (Zhang et al., 2014); and (iii) it suppresses the neuronal response to features, objects, or events that are not selected. In the discussion on the relationship between consciousness and attention, the second aspect of attention, attentional amplification, is most relevant. The third aspect is also critical when attention resolves competition among visual objects.

Since the late nineteenth century, selection is known to be based on either bottom-up, exogenous or top-down, endogenous factors (James, 1890; Braun and Julesz, 1998; Duncan, 1998). Exogenous cues are image-immanent features that transiently attract attention or eye gaze, independent of any particular task. Thus, if an object attribute (e.g., flicker, motion, color, orientation, depth, or texture) differs significantly from its value in some neighborhood, the object will be salient. This definition of bottom-up saliency has been implemented into a popular 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 (Itti and Koch, 2001) (see <http://ilab.usc.edu/toolkit/> for a C++ implementation and <http://www.saliencytoolbox.net/> for a Matlab toolbox). Such algorithms account for a significant fraction of fixational eye movements (Parkhurst et al., 2002; Peters et al., 2005; Mannan et al., 2009). Higher-order features, such as faces and text, also contribute to the computation of global saliency, as these objects strongly attract eye movements in a task-independent manner (Cerf et al., 2009). Candidates for one or more saliency maps in the primate brain include the initial responses of neurons in the frontal eye field (FEF), the lateral or posterior intraparietal sulcus (LIP) (Constantinidis and Steinmetz, 2005; Thompson and Bichot, 2005; Bogler et al., 2011) and in the superficial layers of the superior colliculus (White et al., 2014).

Under many conditions, however, subjects can disregard salient, bottom-up cues when searching for

particular objects in a scene by dint of top-down, task-dependent control of attention ([Henderson et al., 2006](#)). Bringing top-down, sustained attention to bear on an object or event in a scene takes time. Top-down attention selects sensory inputs defined by a circumscribed region in space (*spatial attention*) or time (*temporal attention*), by a particular feature (*feature-based attention*), or by an object (*object-based attention*). It is the relationship between these volitionally-controlled forms of top-down, selective, endogenous attention and consciousness that is the topic of this chapter. (For an evidence that top-down, voluntary spatial attention and bottom-up, involuntary attention interact with consciousness in different manners, see [Hsu et al., 2011](#).)

When considering functions of consciousness, it is useful to distinguish two concepts: “phenomenal consciousness” and “access consciousness” ([Block, 1996, 2007](#)). Phenomenal consciousness is defined as “what it is like to have any one specific experience” and it is closely related to the philosophical concepts of qualia (a quale is the singular form for the Latin word qualia). A representation is access-conscious if it is posed for direct control of reasoning, reporting, and action—that is, those aspects of any experience that can be reported or remembered. Cognitively accessed contents of consciousness are stored for working memory and flexibly guide present and future behaviors. It remains controversial whether phenomenal experience overflows access consciousness.

Many candidate functions for the cognitively accessed contents of consciousness have been proposed, ranging from summarizing all relevant information pertaining to the current state of the organism and its environment and making this compact summary accessible to the planning stages of the brain, to detecting anomalies and errors, decision making, language, inferring the internal state of other animals, setting long-term goals, making recursive models, and logical inference. While all these functions are clearly related to access consciousness, it is not clear how the raw feeling of any one conscious experience, its qualia or phenomenal consciousness, relates to any of the above functions.

Integrated Information Theory (IIT) ([Tononi, 2004; Oizumi et al., 2014](#)) offers a distinctive take on this issue. IIT views information from the point of view of causation. The information content of an experience is specified by the “form” of the associated conceptual structure and quantified by the non-negative number Φ^{\max} . Information is *intrinsic* and *causal*: it is assessed from the intrinsic perspective of a system based on how its mechanisms and present state affect the probability of its own past and future states (intrinsic cause-effect power; [Oizumi et al., 2014](#)). IIT identifies integrated information as the maximal causal-effect power that the system exerts on itself. Maximal cause-effect power is what

consciousness is (an identity relation). IIT argues that organisms with higher Φ^{\max} will experience richer phenomenology and cope with the environment in a more adaptive manner compared to competitors with less integrated information (Φ^{\max}). Indeed, digital organisms (“animats”) whose brains evolve over 60,000 generations by simulated natural selection in a maze show a monotonic relationship between integrated information and adaptation. Similarly, as animats evolved to catch falling blocks in a *Tetris*-like scenario, they increase fitness along with both Φ^{\max} and the number of irreducible causal functions (called “concepts” [Oizumi et al., 2014; Albantakis et al., 2014](#)). Moreover, while in simpler environments, animats with modular, feedforward brains that have zero Φ^{\max} —and therefore no consciousness—can do well, only animats with high Φ^{\max} and therefore a larger capacity for consciousness evolve to adapt to more complex environments ([Edlund et al., 2011; Joshi et al., 2013; Albantakis et al., 2014](#)).

In sum, while the scientific community has relatively clear ideas concerning the putative functions of selective attention, the functions—if any—of phenomenal consciousness remain elusive. However, it is clear that long as attention and consciousness have different biological functions, they cannot be the same processes.

Then, how exactly do they differ, and under what circumstances? Our 2×2 matrix ([Table 5.1](#)) lists four possible ways in which attention and consciousness interact. Each cell contains a particular percept or behavior depending on whether or not it requires top-down attention and whether it necessarily gives rise to consciousness.

THE FOURFOLD WAY OF PROCESSING VISUAL EVENTS

While many scholars agree that attention and consciousness are distinct, some insist that the former is necessary for the latter, and that non-attended events remain subliminal ([Dehaene et al., 2006; Cohen et al., 2012](#)). For example, [Dehaene and colleagues \(2006\)](#) argue that without top-down attentional amplification, an event cannot be consciously perceived (preconscious). The evidence reviewed below argues otherwise, at least for some types of percepts.

More than a century of research efforts have quantified the ample benefits that accrue to attended and consciously perceived events. For example [Mack and Rock \(1998\)](#) compellingly demonstrate that subjects must attend to become conscious of novel or unexpected stimuli. Integrating information over large distances in space and time or across modalities requires attention and consciousness, while neither may be required over smaller distances ([Mudrik et al., 2014](#)).

TABLE 5.1 A Fourfold Classification of Percepts and Behaviors Depending on Whether or Not Top-Down Attentional Amplification Is Necessary for Them to Occur and Whether or Not These Percepts and Behaviors Necessarily Give Rise to Consciousness

	Does not necessarily give rise to consciousness	Is always associated with consciousness
Can occur under limited top-down attentional allocation	Formation of afterimages	Iconic memory
	Rapid vision (<120 ms)	Gist
	Zombie behaviors	Animal and gender detection in dual tasks
	Storing primitive information for short durations	Partial reportability
	Basic summary statistics (e.g., size and number)	
	Local, weak integration of information	
Requires top-down attention	Pop-out	Storing information in working memory for flexible use
	Priming	Detection and discrimination of unexpected and unfamiliar stimuli
	Adaptation	Full reportability
	Processing of objects	Global, strong integration of information
	Visual search	
	Thoughts	
	Eye-of-origin information	

The items placed in the lower right quadrant of our attention \times consciousness design matrix (Table 5.1) require selective top-down attention and will give rise to a conscious experience.

On the other end of the spectrum are visual behaviors that can occur without the need of top-down attention and that may not give rise to consciousness. These may be supported by predominantly feedforward processing, composed of a net-wave of spiking activity moving from the retina into primary visual cortex and beyond. They can be also triggered by previously trained sensory-motor activity that is mediated by feedforward processing. Further, reverberating neuronal activity that remains confined to the primary visual cortex and never arrives high-level association cortex can also produce these percepts and behaviors. Such processing, that is not amplified by top-down attention and does not give rise to consciousness, however, can still be causally effective and leave traces that can be picked up with sensitive behavioral techniques. For instance, such stimuli can subsequently cause negative afterimages (Hofstoetter et al., 2004; Tsuchiya and Koch, 2005; Gilroy and Blake, 2005; Brascamp et al., 2010; van Boxtel et al., 2010b). These occupy the upper left quadrant of Table 5.1.

Working memory stores information for a short period of time, up to several seconds, so that the information can be manipulated for future use in a flexible fashion. Many cognitive neuroscientists assert that actively stored items are perceived consciously and selected by attention, placing working memory in the bottom right quadrant of Table 5.1 (Baars and Franklin, 2003). However, some form of short-term, flexible storage of stimulus information is also possible without consciously seeing the stimulus or attending to it. Monkeys whose primary visual cortex has been removed exhibit blindsight behaviors as do patients (Takaura et al., 2011): when forced, the monkeys can make saccades to a target presented in the blind field accurately. Surprisingly, the lesioned monkeys can also saccade to the target location, even after the target vanishes from the display up to 2.4 s (Takaura et al., 2011). Healthy human volunteers can also retain information about the orientation of a masked invisible stimulus and use it as a template for subsequent orientation discrimination (Soto et al., 2011; see also Soto and Silvanto, 2014 and Hassin et al., 2009). These recent studies call into question the relationship between attention and consciousness as necessary sub-components of working memory.

When subjects are briefly shown a group of objects in a display, some basic summary statistics, such as the average size or the number of elements, are behaviorally accessible without attention. Computing the average or counting objects proceeds before selective attention can be deployed (Oriet and Brand, 2013). Furthermore, perceptually invisible, masked objects also contribute to the estimation of the mean size and numerosity (Choo and Franconeri, 2010). As far as we know, however, an orthogonal 2×2 manipulation of attention and consciousness has not yet been performed to investigate the nature of statistical perception.

What about the two remaining quadrants, covering events that require top-down attention but that do not necessarily give rise to conscious perception, and events that can give rise to consciousness without top-down attentional amplification? These can be studied with techniques that independently manipulate top-down attention and visual consciousness (Boxes 5.1 and 5.2).

ATTENTION WITHOUT CONSCIOUSNESS

Much neuronal processing causes observable motor behavior without giving rise to consciousness (Hassin et al., 2005). The implicit effects of such non-conscious processing can be revealed by careful psychophysical probing. After prolonged viewing of some sensory stimuli, subjects exhibit reduced sensitivity to the same stimulus presented afterwards, a phenomenon called an *aftereffect*. Interestingly, even if the stimulus is not consciously perceived, strong aftereffects can be induced (Blake and Fox, 1974; Blake et al., 2006). In *priming*, briefly presented stimuli influence subsequent behaviors. Some types of priming can occur even when priming stimuli remain invisible (Kouider and Dehaene, 2007). This non-conscious processing, however, can be strongly modulated by the availability of top-down attention or can be completely eliminated when top-down attention is directed away from stimuli that induce the non-conscious percepts and behaviors (lower left quadrant in Table 5.1).

In *visual crowding*, the orientation of a peripherally-presented grating can be rendered inaccessible to consciousness by neighboring gratings. Here, the surrounded target grating can be detected consciously, yet its tilt angle cannot be discriminated at all. The central target grating, therefore, is above the detection and below the discrimination threshold, a classic example of “partial awareness” (Kouider et al., 2010). This crowded grating, however, remains sufficiently potent to induce an orientation-dependent aftereffect (He et al., 1996). A similar aftereffect can be induced

by an indiscriminable grating defined by illusory contour (Montaser-Kouhsari and Rajimehr, 2005). This aftereffect depends strongly on the availability of top-down spatial attention: it can only be induced when subjects actively try to attend to the orientation of the indiscriminable grating (Montaser-Kouhsari and Rajimehr, 2005). Naccache and colleagues (2002) elicited priming for invisible flashed words (suppressed by a combination of forward and backward masking) but only if the subject was attending to the invisible prime-target pair at the appropriate time; without temporal attentional amplifications, the invisible word failed to elicit priming.

Attention without consciousness has been investigated using stimuli that themselves do not give rise to consciousness (Rajimehr, 2004; Norman et al., 2013). To achieve reliable and prolonged invisibility a technique, called continuous flash suppression or CFS for short, is often used (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006; Yang and Blake, 2012). In CFS, an image is presented to one eye, which is rendered invisible for seconds to minutes (Tsuchiya and Koch, 2005) by flashing randomly generated, edge-rich, stimuli to the other eye at around 10 Hz in the corresponding retinal location. The potency of such invisible stimuli to attract bottom-up attention has been a particular focus of research. Using CFS, invisible male/female nudes have been shown to attract covert attention (Jiang et al., 2006). Interestingly, in heterosexuals, these effects are only apparent for nudes of the opposite sex. Note that by themselves (i.e., without the binocular mask), these stimuli are clearly visible. Another study using CFS revealed that pop-out target can attract bottom-up attention even if the entire stimulus array itself is rendered invisible (Hsieh et al., 2011). However, this non-conscious pop-out effect depends on top-down spatial attention: when distracted by another task at the fixation, this pop-out effect disappears (Hsieh et al., 2011). Not only spatial attention but also feature-based attention can spread to and act on invisible stimuli (Melcher et al., 2005; Kanai et al., 2006). 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. 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 and are therefore invisible to him (Kentridge et al., 1999a,b, 2004).

Although visual information enters the brain separately through the two eyes, subjects have very poor conscious access to “eye-of-origin” information when information is presented to one eye only—that is, “did

PSYCHOPHYSICAL TOOLS TO MANIPULATE TOP-DOWN ATTENTION

Top-down attention and consciousness are usually tightly coupled. To dissociate these two, experimental tools that manipulate either one independently in a specific manner with few side effects are called for.

There exist at least two forms of selective attention: stimulus-driven, bottom-up, saliency-mediated attention as well as task- and goal-dependent top-down attention, with some intermediate forms. Previously neutral stimuli (such as text, or images of guns) can be associated with reward or punishment to acquire additional saliency. Biologically relevant stimuli may be preferred or disliked based on individual difference (e.g., snakes, spiders, sexual arousing pictures).

A variety of techniques to manipulate these components of attention have been invented. It is not always easy to compare them, as each method interferes with attention at a different level of processing (Sperling and Doshier, 1986; VanRullen et al., 2004).

In Posner's cueing paradigm, popular to study orienting (Posner et al., 1980), a target is preceded by a cue that appears at the target location or at fixation. Attentional effects are inferred in terms of reaction time and accuracy of target detection. Variants of the methods demonstrated that invisible cue can direct attention to the cued location (Jiang et al., 2006; McCormick, 1997; Rajimehr, 2004; Sumner et al., 2006; Kentridge et al., 2004), supporting attention without consciousness. A study by Kok and colleagues (2012), however, casts doubt on a large body of Posner-type manipulations that manipulated the probability that a cue predicts the target location; these studies might have confounded attention with expectation, both of which are likely to have distinct biological functions and underlying mechanisms (Summerfield and Egner, 2009).

In visual search, subjects need to find a target among distractors; reaction time is related to the number of distractors. When the search slope is steep, the search process is said to be *serial*, and when flat, *parallel*. The former is usually taken as the evidence of serial processing by top-down attention. However, the steep serial search may arise due to completely bottom-up factors (Wolfe, 1998). This exemplifies a case where dual tasks and visual search methods may yield inconsistent results.

The *dual-tasks paradigm* (Sperling and Doshier, 1986; Braun and Julesz, 1998; Braun and Sagi, 1990) 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 stimulus is projected somewhere into the periphery. Subjects either carry out the central, the peripheral or both tasks simultaneously while the scene and its layout remains the same. Surprisingly, seemingly

complex peripheral tasks can be done equally well under either single-task or dual-tasks condition, while other, computationally simpler, tasks deteriorate when performed simultaneously with the central task (Figure 5.2). The dual-tasks paradigm quantifies what type of stimulus attributes can be performed under no or little spatial attention (VanRullen et al., 2004).

Most importantly, the dual-tasks paradigm can be easily combined with a multitude of visual illusions that render stimuli invisible, allowing the independent manipulation of top-down attention and consciousness (Watanabe et al., 2011; van Boxtel et al., 2010b).

The inference of attentional requirements from dual-tasks performance demand a caution. High proficiency in such tasks is only achieved after extensive training of many hours. Such an extended training phase may render the task quite different from what naïve subjects do (Braun, 1998; Joseph et al., 1997) and may well reflect the involvement of different brain regions.

Finally, there is a class of neurological conditions as well as visual illusions in normal subjects where stimuli become invisible because of impairments in the mechanisms of top-down or bottom-up attention. Neglect and extinction (Driver and Mattingley, 1998), attentional blink (Raymond et al., 1992; Chun and Potter, 1995), inattention blindness (Mack and Rock, 1998), and change blindness (Simons and Rensink, 2005) are sometimes used as positive evidence for "without attention, no consciousness" (O'Regan and Noe, 2001). Although some attributes of the visual input need attentional amplification to rise to the level of consciousness, other aspects, such as the gist of the scene and its emotional content, are quite resistant to such attentional manipulations (Mack and Rock, 1998; Anderson and Phelps, 2001).

Cohen and colleagues (2012) argue that four different psychophysical techniques—attentional blink, inattention blindness, change blindness and the dual-task—should be used in conjunction to test whether or not consciousness without attention is possible. They argue that in some of these conditions, even faces and natural scene cannot be perceptually experienced if top-down attention fail to amplify the signal. It is unclear, however, how much of "blindness" in these phenomena is due to the lack of top-down attentional amplification. Attentional blink, inattention blindness, and change blindness are composed of distinct cognitive processes, such as backward masking, memory consolidation (Wolfe, 1999), and expectation (Braun, 2001; Summerfield and Egner, 2009; Kok et al., 2012). Some of these non-attentional components may play a more significant role than the top-down selective attentional amplification in mediating perceptual blindness in these situations (Tsuchiya and Koch, 2014).

BOX 5.2

HOW TO MEASURE VISUAL CONSCIOUSNESS

Visual consciousness can be manipulated using a multitude of illusions, such as backward masking, the standing wave of invisibility ([Macknik and Livingstone, 1998](#)), crowding, bistable figures, binocular rivalry, flash suppression, continuous flash suppression, motion-induced blindness, chromatic flicker fusion ([Jiang et al., 2007](#)), and attentional blink (for a review see [Kim and Blake, 2005](#)). These techniques control the visibility of an object or part of thereof in both space and time. Yet how is visibility assayed? More generally, how can the degree of consciousness be probed?

The most lenient criterion is to accept what subjects subsequently report verbally (e.g., “I never saw the face”). Though widely used, such as when obtaining reports right after a block of trials, this method is unsatisfactory because unattended items or task-irrelevant (implicit) features of stimuli may be inaccessible in subsequent recognition or recall tasks, called inattentional amnesia ([Wolfe, 1999](#); [Lovibond and Shanks, 2002](#)). A more stringent criterion for non-conscious processing is to ask subjects about their experience directly at the time the stimulus is processed. When subjects deny seeing stimuli, the stimulus is processed at a *subjectively non-conscious* level. Although many studies adopt this convention, it suffers from a possibility of individual differences in decision criteria; for the same subjective experience of visibility, some subjects may deny seeing a stimulus while others may report seeing it, because their criterion of what to count as “seen” differs.

Taking into account criterion differences, one can compute signal discriminability (or d') within the framework of signal detection theory. When subjects show no discriminability ($d' = 0$) for a stimulus, it can safely be assumed that they are not conscious of that particular stimulus dimension being tested for (e.g., male vs female face gender discrimination). A recently developed Bayesian framework estimates how convincing the demonstrated invisibility is ([Dienes, 2011](#)). For example, subjects can be given two alternative temporal intervals (or locations), each of which contains the stimulus equally often. In this procedure, care needs to be taken to intermix trials of low and high visibility to keep subjects motivated ([Lin and Murray, 2014](#)). If observers perform at chance in detecting/discriminating one from the other, they are (objectively) unaware of the stimulus (our use of “subjective” and “objective” here refers to the method used, not to the nature of the conscious experience, which is of course always subjective in terms of its phenomenology). When these protocols are used

carefully, there is excellent agreement between objective and subjective measures of consciousness ([Del Cul et al., 2007](#)). Note that above-chance behavioral discrimination performance does not necessarily demonstrate conscious awareness, since patients with blindsight exhibit precisely such performance.

Objective-performance-based definitions of consciousness, however, are flawed because they do not directly reflect phenomenal experience, which is the central issue. By applying the objective measure of signal discriminability to one’s own judgment of whether the stimulus is seen or not, one can *objectively* measure *subjectivity*. That is, one can consider the discriminability (d') of one’s own experience, a form of metacognition. For this method, subjects first make a detection/discrimination judgment, then rate the confidence in their decision. Defining “hit” as proportion of high-confidence ratings given the decision was correct— $p(\text{high confidence} | \text{correct})$ —and “false alarm” as the proportion of high-confidence ratings given the decision was incorrect— $p(\text{high confidence} | \text{incorrect})$ —one can calculate the signal discriminability. In signal detection theory, this is called Type 2 analysis, which has been applied to evaluate above-chance behavior in non-conscious perception ([Kolb and Braun, 1995](#); [Kunimoto et al., 2001](#); [Szczepanowski and Pessoa, 2007](#); [Galvin et al., 2003](#); [Maniscalco and Lau, 2012](#); [Kanai et al., 2010](#); [Barrett et al., 2013](#)).

Reflecting upon one’s own judgment may require substantial internal focus, and such an act itself can modify conscious experience significantly ([Maia and McClelland, 2004](#)). *Post-decision wagering* minimizes this contamination due to introspection ([Kunimoto et al., 2001](#); [Persaud et al., 2007](#)). Following each response, subjects wager on their performance, betting either high or low. When the subject is confident that she saw the stimulus, reward maximization would presume that she would wager a higher amount than when she is unaware of the stimulus. Here, subjects’ awareness is gauged by their discriminability of their own judgment. This method proves to be easy and intuitive for subjects to use and very effective in reflecting one’s subjective aspects of consciousness while minimizing interference to the quality of the experience. [Persaud and colleagues \(2007\)](#) observed non-conscious, above-chance behaviors in blindsight patients, implicit learning, and Iowa gambling task while demonstrating non-conscious access to the information by post-decision wagering. Note, however, the post-decision wagering is subject to loss- or risk aversion, a concept in behavioral economics,

BOX 5.2 (cont'd)

which needs to be carefully teased apart from the effects of conscious phenomenology ([Wang et al., 2012](#); [Sandberg et al., 2010](#); [Clifford et al., 2008](#); [Dienes and Seth, 2010](#); [Koch and Preusschoff, 2007](#); [Fleming and Dolan, 2010](#); [Schurger and Sher, 2008](#)).

While confidence rating and post-decision wagering asks subjects to rate their confidence in their perceptual “decisions,” the perceptual awareness scale (PAS) ([Ramsøy and Overgaard, 2004](#); [Sandberg et al., 2010, 2011](#)) directly asks subjects to describe their qualitative experience on a scale from “no experience,” to “brief glimpse,”

“almost clear image” to “absolutely clear image.” All methods referred here (confidence rating, post-decision wagering, and PAS) can be used to compute the accuracy of metacognition. Furthermore, by focusing on the trials in which subjects reported invisibility of the stimulus, metacognitive accuracy about invisibility judgment can be assessed. ([Kanai et al., 2010](#)).

As the study of consciousness matures, the methodological development in how to assess consciousness continues to be refined and more sophisticated ([Seth et al., 2008](#)).

I see that stimulus with my left or my right eye?” ([Wolfe and Franzel, 1988](#); [Schwarzkopf et al., 2010](#)). However, an odd-ball stimulus defined by the eye-of-origin attracts involuntary, bottom-up attention ([Ooi and He, 1999](#); [Zhaoping, 2008](#)). Furthermore, subjects can prolong or shorten the duration of invisibility of a target stimulus suppressed by CFS by voluntarily attending to a cue that is projected to either the same or opposite eye as the suppressing Mondrian patterns ([Zhang et al., 2012](#)). That is, consciously inaccessible eye-of-origin information can guide voluntary, top-down attention to select and modulate incoming visual information ([Zhang et al., 2012](#)).

In conclusion, attentional selection does not necessarily engender phenomenal conscious sensations, although it may often do so. Attention without consciousness has been demonstrated with both top-down and bottom-up as well as spatial, temporal, feature-based, object-based ([Norman et al., 2013](#)) as well as eye-based attention across many different stimuli and tasks (for reviews, see [Dehaene et al., 2006](#); [van Boxtel et al., 2010a](#); [Cohen et al., 2012](#)). By last count, at least 40 experiments report such an effect ([Tsuchiya and Koch, 2014](#)). Collectively, they demonstrate that the neuronal mechanisms that support these attentional effects are, by themselves, insufficient to give rise to consciousness.

CONSCIOUSNESS IN THE ABSENCE OF ATTENTION

Yet the converse can also occur and may be quite common (upper right quadrant in [Table 5.1](#)). Take perception of a single object (say a bar) in an otherwise empty display, a non-ecological but common arrangement in many experiments. Here, what function would top-down, selective attention need to perform without any competing item in or around fixation? Indeed, the most popular

neuronal model of attention, *biased competition* ([Desimone and Duncan, 1995](#)) predicts that in the absence of competition, no or little attentional enhancement occurs.

Gist Perception

When focusing intensely on one event, the world is not reduced to a tunnel, with everything outside the focus of attention gone. Rather, visual processing at the para-fovea, extending to the periphery, efficiently encodes the statistical properties of the visual fields ([Freeman and Simoncelli, 2011](#); [Rosenholtz et al., 2012](#)). As a result, a concise summary, or gist, of the world surrounding us seems always consciously accessible. Indeed, gist of the scene is immune from inattentional blindness ([Mack and Rock, 1998](#)); when a photograph covering the entire background is briefly flashed completely unexpectedly onto a screen, subjects can accurately report a summary of what it contains. In the 30 ms necessary to apprehend the gist of a scene ([Biederman, 1972](#); [Fei-Fei et al., 2007](#)), top-down attention cannot play much of a role (because gist is a property associated with the entire image, any process that locally enhances features is going to be only of limited use). Perception of gist is a highly vivid, yet coarse, conscious sensation ([Campana and Tallon-Baudry, 2013](#)) ([Figure 5.1](#)).

Dual-Tasks Paradigm

In a dual-tasks paradigm, the subject’s attention is drawn to a demanding central task, while at the same time a secondary stimulus is flashed somewhere in the periphery (see [Box 5.1](#)). Using the identical retinal layout, the subject either performs the central task, or the peripheral task, or both simultaneously ([Sperling and Doshier, 1986](#); [Braun and Julesz, 1998](#); [Braun and Sagi, 1990](#)). With focal attention busy at the center, the subject can still distinguish a natural scene containing

an animal (or a vehicle) from one that does not include an animal (or a vehicle) while being unable to distinguish a red-green bisected disk from a green-red one (Li et al., 2002). Likewise, subjects can tell male from female faces or distinguish a famous from a non-famous face (Reddy et al., 2004, 2006), but are frustrated by tasks that are computationally much simpler (e.g., discriminating a rotated letter “L” from a rotated “T”) (see Figure 5.2 for other perceptual attributes tested in the dual-tasks paradigm).

While we cannot be sure that observers do not deploy some limited amount of top-down attention in

these dual-tasks experiments that require training and concentration (that is, high arousal), it remains true that subjects can perform certain discriminations but not others with no or little top-down attentional amplification.

OPPOSING EFFECTS OF CONSCIOUSNESS AND ATTENTION

The More You Attend, the Less You See

In most conditions, paying attention improves the processing of stimuli, typically their identification or discrimination. Under certain conditions, however, conscious detection of a target can be impaired when subjects pay attention to the target.

When observers try to find two embedded targets within a rapidly flashed stream of stimuli, they often fail to see the second target, a phenomenon known as the *attentional blink* (Raymond et al., 1992; Chun and Potter, 1995). Counter-intuitively, Olivers and Nieuwenhuis (2005) found that observers can see both the first and the second targets better when they are distracted by a simultaneous auditory task or encouraged to think about task-irrelevant events. Surprisingly, relaxing has been also shown to improve visual search, especially when the search is very difficult but not when the search is easy (Smilek et al., 2006). Even in a simple low-level detection task, low spatial frequency stimuli can be better discriminated without than with spatial attention (Wong and Weisstein, 1982, 1983; Yeshurun and Carrasco, 1998).

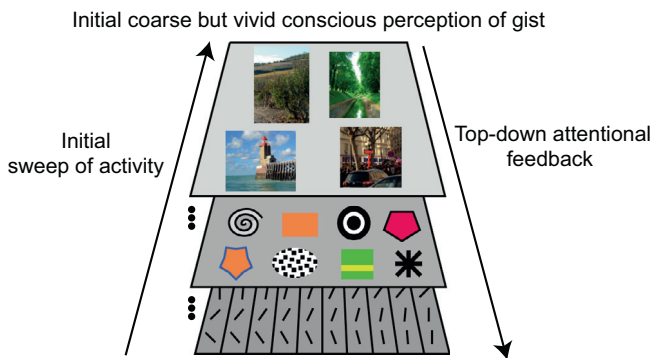


FIGURE 5.1 The coarse vividness hypothesis by Campana and Tallon-Baudry (2013). The initial sweep of activity processed through the ventral visual pathway may be sufficient to give rise to integrated and meaningful conscious perception of gist. However, this coarse representation lacks a detailed description of the scene (e.g., exact spatial locations of an object) which requires top-down attentional feedback. In this view, the perception of gist is a prime example of vivid and coarse consciousness without top-down attention.

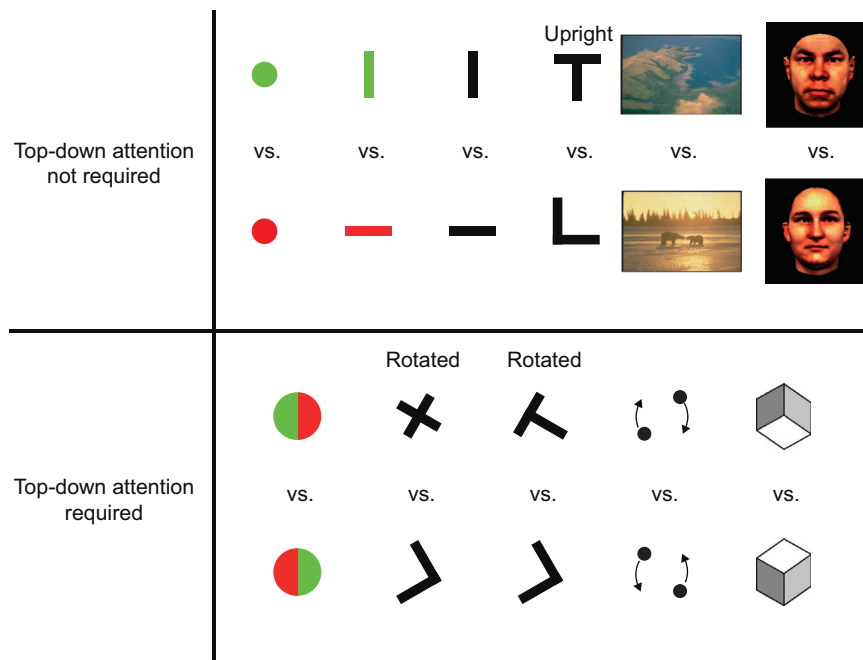


FIGURE 5.2 Various types of visual discriminations and their dependency on top-down attention. The top panel lists perceptual discriminations that require no or little top-down attention (color, orientation, conjunction of color and orientation, upright letters, scene gist, gender, and identity of faces), while the bottom row lists those that require substantial amount of top-down attention (red/green vs. green/red bisected discs, rotated letters, rotation directions of balls, lighting from upwards or downwards), as assessed by the dual-tasks paradigm. This protocol compares discrimination performance of an identical retinal stimulus when fully and when poorly attended (Braun and Julesz, 1998; Lee et al., 1999; Li et al., 2002; Reddy et al., 2004, 2006; VanRullen et al., 2004; Fei-Fei et al., 2005).

These cases imply that focally attending to the task in space or time alters neuronal processing, yet it can impair conscious detection of target.

Impaired task performance due to attention occurs in everyday life as well. Athletes performing their high-performance skills can do better under skill-irrelevant dual-tasks conditions (i.e., paying attention to tones) than when paying attention to their exhaustively trained behaviors ([Beilock et al., 2002](#)). Similar effects are reported even in non-athletes during keyboard typing ([Logan and Crump, 2009](#)).

While top-down attention usually facilitates perceptual learning of task-relevant stimuli, it can interfere with task-irrelevant and implicit learning ([Choi et al., 2009](#)). Attending to a location impedes task-irrelevant perceptual learning ([Choi et al., 2009](#)). During implicit learning, attentively trying to discover the underlying complex rule delays learning and impairs subsequent recognition ([Reber, 1976](#)). Recognition memory can decrease when the subject's attention is directed to the task-relevant complex kaleidoscopic visual stimulus under certain circumstances ([Voss et al., 2008](#); [Voss and Paller, 2009](#)).

Finally, a more direct demonstration of “the more you attend, the less you see” comes from several visual illusions. In *motion-induced blindness* ([Bonneh et al., 2001](#)), a salient target can be rendered invisible when it is surrounded by moving dots. Here, the more salient, bottom-up attention-grabbing the stationary yellow targets are, the longer the suppression ([Bonneh et al., 2001](#)). Furthermore, when more top-down spatial attention is paid to the salient targets, they disappear faster ([Geng et al., 2007](#); [Schölvinck and Rees, 2009](#)). In *Troxler fading* ([Troxler, 1804](#)), a stimulus placed in the visual periphery fades from view when fixation is held correctly. This fading happens faster when attention is directed to the peripheral stimulus ([Babington-Smith, 1961](#); [Lou, 1999](#)). Similarly, *afterimages* ([Bachmann and Murd, 2010](#)) as well as *motion aftereffects* ([Murd and Bachmann, 2011](#)) disappear faster when spatial attention is directed to see them better. In all of the above cases, the more subjects try to experience a percept vividly by paying attention to it, the less visible it becomes!

Independent Manipulation of Attention and Consciousness

Recently, researchers have started manipulating consciousness and attention independently using the same stimuli within a single paradigm in perceptual and behavioral tasks ([Kanai et al., 2006](#); [van Boxtel et al., 2010b](#); [Van den Bussche et al., 2010](#)) (see [Boxes 5.1 and 5.2](#)). These studies typically manipulate the conscious visibility of a target stimulus via backward, lateral or inter-ocular masking ([Kim and Blake, 2005](#);

[Tsuchiya and Koch, 2005](#)); if the stimulus is not seen and not reported on, it is not consciously perceived. At the same time, top-down attention is manipulated using a dual-task design.

When manipulated independently in this manner, consciousness and attention affect the duration of afterimages in opposing ways ([van Boxtel et al., 2010b](#)). A number of experiments showed, paradoxically, that attending to a stimulus reduces the duration of its induced afterimage ([Suzuki and Grabowecky, 2003](#); [Lou, 2001](#); [Wede and Francis, 2007](#); [Lak, 2008](#); [Baijal and Srinivasan, 2009](#)) and, independently, that perceptual invisibility of a stimulus reduces the duration of afterimage ([Tsuchiya and Koch, 2005](#); [Gilroy and Blake, 2005](#)). Because the effects of consciousness depend on the details of the afterimage-inducing stimulus (e.g., spatial frequency [Brascamp et al., 2010](#)), it is critical to use the same stimuli to study the effects of consciousness and attention.

These opposing perceptual effects of attention and consciousness become easier to understand if the neuronal mechanisms that support them are largely independent and can be dissociable ([Tallon-Baudry, 2011](#)). Indeed, neuroimaging and neurophysiological studies have started uncovering the neuronal basis of attention and consciousness to be highly dissociable when each is manipulated independently.

NEURONAL MEASURES OF DISSOCIATIONS BETWEEN ATTENTION AND CONSCIOUSNESS

The neuronal footprints of non-conscious processing of visual information have been tracked using both event-related potentials and functional magnetic resonance imaging (fMRI; for a review see [Dehaene and Changeux, 2011](#)). Only recently have such tools been applied to separate the neuronal mechanisms of top-down attention from conscious and non-conscious processing ([Woodman and Luck, 2003](#); [Koivisto et al., 2006](#); [Koivisto et al., 2005](#); [Bahrami et al., 2007](#); [Tsushima et al., 2006](#); [Lee et al., 2007](#); [Watanabe et al., 2011](#); [Wyart and Tallon-Baudry, 2008](#)).

Neurophysiological evidence for attention without consciousness came from a fMRI study ([Bahrami et al., 2007](#)), demonstrating that the processing of objects hidden from sight (with $d' = 0$, or no possibility to detect stimulus above chance (see [Box 5.1](#))) via continuous flash suppression depended on the availability of spatial attention. Bahrami and colleagues varied the load of the central task in a dual-task design. The hemodynamic blood-oxygen-level-dependent (BOLD) response to the invisible, peripheral objects in primary visual cortex, V1, was stronger when the central task was easy, that is, when spatial attention was available for processing the invisible, peripheral stimulus than

when the central task was hard and more attentional resources were drawn to it. In other words, attention modulates the fMRI response of an invisible stimulus.

Watanabe and colleagues (2011) employed a 2×2 factorial design to independently manipulate consciousness and attention while recording fMRI signals from the primary visual cortex (V1) in humans. They found that the V1 hemodynamic response is strongly modulated by spatial attention, consistent with (Bahrami et al., 2007), but not by the conscious visibility of a grating, consistent with (Crick and Koch, 1995). Similar effects have been reported for neuronal activity recorded via microelectrodes from monkey V1 (Maier et al., 2011). These two experiments challenge many previous fMRI studies (Polonsky et al., 2000; Haynes et al., 2005; Wunderlich et al., 2005) that used binocular rivalry and located the neuronal correlates of consciousness to V1 and even the lateral geniculate nucleus of the thalamus (also see Maier et al., 2008 on the difference between single neuron activity and hemodynamic response in monkey V1). A recent study (Yuval-Greenberg and Heeger, 2013) reported significant effects of stimulus visibility in V1 fMRI BOLD activity using CFS, unlike the earlier study by Watanabe and colleagues. The overall design is similar except that Yuval-Greenberg and Heeger used three times more trials per subjects than the earlier experiment. Yet even if there is a statistically significant effect of visibility on V1 BOLD activity, our central conclusion remains the same: selective attention modulates V1 activity more so than stimulus visibility (standing in for conscious awareness of the stimulus) during binocular rivalry and CFS.

The controversy over fMRI studies with binocular rivalry and CFS exemplifies the necessity of separating consciousness from attention; unless explicitly manipulated independently, the neuronal correlates of consciousness can, and usually will, co-vary with the neuronal correlates of attention (Tse et al., 2005; Koch and Tsuchiya, 2012).

An even more paradoxical effect—that invisible stimuli can be more distracting than visible ones—was discovered by Tsushima and colleagues (2006). In this study, subjects had to detect foveally-placed targets in a stream of characters—a *rapid serial visual presentation* task—surrounded by an annulus of moving dots. The fraction of dots moving coherently in one direction (motion coherence)—was varied from 0% (truly random dot motion) to 50% (half of the dots move in the same direction). When the central task was combined with the task-irrelevant surround motion, the central performance *dropped* when the coherent motion was perceptually below threshold (say at 5%, where the cloud of dots was not perceived to move coherently) compared to when the motion coherence was 0% or above threshold (e.g., 20%). This counterintuitive finding was explained by the parallel fMRI study in which the authors looked

at BOLD activity in area MT+, which reflects the degree of distraction by motion stimuli, and in the lateral prefrontal cortex (LPFC), which provides an attentional suppression signal to MT+. Compatible with the behavioral findings, invisible motion did not elicit activity in the LPFC, resulting in higher distractor-related activity in MT+. On the other hand, visible motion evoked a stronger LPFC signal but a weaker MT+ one. The authors hypothesize that invisible motion activates MT+, impairing performance, but not the LPFC, which fails to inhibit MT+; thereby stimuli that are not consciously perceived can escape inhibitory control, a phenomenon more familiar from psychoanalysis than from sensory psychology.

Using faint stimuli, Wyart and Tallon-Baudry (2008) also performed 2×2 manipulation of spatial attention (cued or not cued) and consciousness (visible or not visible). Their magnetoencephalographic signals revealed independent neural correlates of visual awareness (54–64 Hz, 240–250 ms post stimulus) over the contralateral visual cortex, regardless of the location of attention, and spatial attention (76–90 Hz, 350–500 ms post stimulus) over parietal cortex, regardless of stimulus visibility.

Finally, the neural signatures of consciousness are also being sought in the absence of attentional selection and read-out in an inattentional blindness paradigm (Pitts et al., 2012; Pitts et al., 2014). Vandenbroucke and colleagues (2014) were able to classify non-reported visual percepts—here a group of Pack-man icons that induced illusory Kanizsa figure from other groups of stimuli that did not induce illusory percept—via multi-voxel pattern analysis in visual topographic regions. Remarkably, the unique neural signature for the non-reported Kanizsa figure was observed in the subjects who were subsequently able to report the figure as well as in those who could not, that is, who were inattentionally blind. This result is consistent with an idea that stimuli that are not cognitively accessed are still perceptually interpreted, up to the representation of illusory surfaces.

RELATIONSHIP TO OTHER CONCEPTUAL FRAMEWORKS FOR TOP- DOWN ATTENTION AND CONSCIOUSNESS

How do these experimental dissociations of top-down attention and consciousness relate to dominant models, theories, and conceptual frameworks in cognitive neuroscience?

When we attend to a face or to an object within a cluttered scene, we usually become conscious of its attributes, with all of the attendant privileges of consciousness (e.g., access to working memory and, in linguistic competent individuals, verbal reportability).

While the minimal neuronal mechanisms jointly sufficient for any one conscious visual percept remain elusive, a number of models posit that they must involve neuronal populations in extra-striate visual cortices having a reciprocal relationship—mediated by long-range cortico-cortical feedforward and feedback projections—with neurons in parietal, temporal, and prefrontal cortices (Tononi and Edelman, 1998; Lamme and Roelfsema, 2000; Crick and Koch, 2003; Dehaene et al., 2003; Baars, 2005). Furthermore, a number of elegant fMRI experiments (Haynes and Rees, 2005; Lee et al., 2007) are consistent with the hypothesis that primary visual cortex (V1) is necessary, but not sufficient for visual consciousness (Crick and Koch, 1995).

Decades of electrophysiological recordings in monkeys have proven that the spiking responses of neurons in the ventral visual stream (e.g., in areas V4 and IT) representing attended stimuli are boosted at the expense of the response to non-attended items (Desimone and Duncan, 1995). According to Crick and Koch (1995), this enables these neurons to establish a reciprocal relationship with neurons in the dorsolateral prefrontal cortex and related regions that are involved in working memory and planning (and language in humans), leading to reverberatory neuronal activity that outlasts the initial stimulus duration. Critical to the formation of such a single and integrated coalition of neurons are the long-range axons of pyramidal neurons that project from the back to the front of cortex and their targets in the front that project back to the upper stages of the ventral pathway (possibly involving stages of the thalamus, such as the pulvinar (Crick and Koch, 1998)) as well as the claustrum (Crick and Koch, 2005; Koubeissi et al., 2014). When such a wide-ranging coalition has established itself, the subject becomes conscious of its representational contents and gains access to short-term memory, planning, and language generation stages.

But what happens to those stimuli that do not benefit from attentional boosting? Depending on the exact circumstances (visual clutter in the scene, contrast, stimulus duration) these stimuli may likewise establish coalitions of neurons, aided by local (i.e., within the cortical area) and semi-local feedback (i.e., feedback projections that remain consigned to visual cortex) loops. However, as these coalitions of neurons lack coordinated support from feedback from prefrontal cortex, thalamus, and claustrum, their firing activity is less vigorous and may decay much more quickly. Yet aided by the neuronal representation of the entire scene, these weaker and more local coalitions may still be sufficient for some phenomenal consciousness (Block, 1996, 2007; Lamme, 2006, 2010), even though the associated coalition does not reach into the front of the brain to enable access consciousness for verbal or motor report or working memory (Frässle, 2014). In other words, for visual phenomenal

consciousness, coalitions in the back of the cortex might be sufficient, while access consciousness might require the associated coalition to reach into the frontal lobe.

Block (2007, 2011, 2012) has argued that phenomenally conscious states may sometimes not be cognitively accessible, in the sense that they are consciously experienced but that subjects may only have limited access to their attributes as assayed by recall or alternative-forced choice judgments. This view captures not only the general experience that “we see much more than we can report upon” but also verbal reports from subjects participating in the classical iconic memory experiment (Sperling, 1960; Landman et al., 2003). That is, a discrepancy between the vivid, conscious impression of a field of letters or bars arranged on a circle on the one hand and limited access to the detailed properties of the individual elements on the other hand (unless top-down attention is directed to a subset of stimuli using appropriate cues). In this sense, the phenomenal impression of a field of whole letters without being able to access each individual element making up this experience (for instance, the identity and location of every letter in the entire display) may be an instance of what we have been calling consciousness without top-down attention (Koch and Tsuchiya, 2008). Note, however, that the converse is not true. Consciousness without top-down attention, such as faces presented in the periphery in a dual-task, can be phenomenally experienced and cognitively accessed. A related concept is the “coarse and vivid” hypothesis by Campana and Tallon-Baudry (2013).

While phenomenology without any cognitive access is hard to establish, the neuronal effects of cognitive access can be deduced by employing a no-report paradigm, which has been gaining popularity in recent neuroimaging and neurophysiological studies (Frässle et al., 2014; Wilke et al., 2009; Vandenbroucke et al., 2014; Pitts et al., 2012; Pitts et al., 2014). In these studies, an initial experiment establishes the neural activity that is correlated with concurrent subjective and objective reports, for instance, during binocular rivalry. Subsequently, this neural activity is contrasted with the activity recorded under the same experimental setup, but now, without overt subjective reports, reducing the effects of cognitive access. With this no-report paradigm, Frässle and colleagues (2014) found that right frontal cortical activation during binocular rivalry, which had been previously claimed as the central neural correlate of consciousness (Rees, 2001; Bor and Seth, 2012; Dehaene and Changeux, 2011), is abolished by eliminating the act of reporting. Note, however, that even without reports, subjects continue to experience binocular rivalry and that their perceptual switches can be decoded by objective eye movements (Figure 5.3). No-report paradigms will be critical to distinguish the core neuronal correlates of phenomenal consciousness from neuronal pre-requisites or

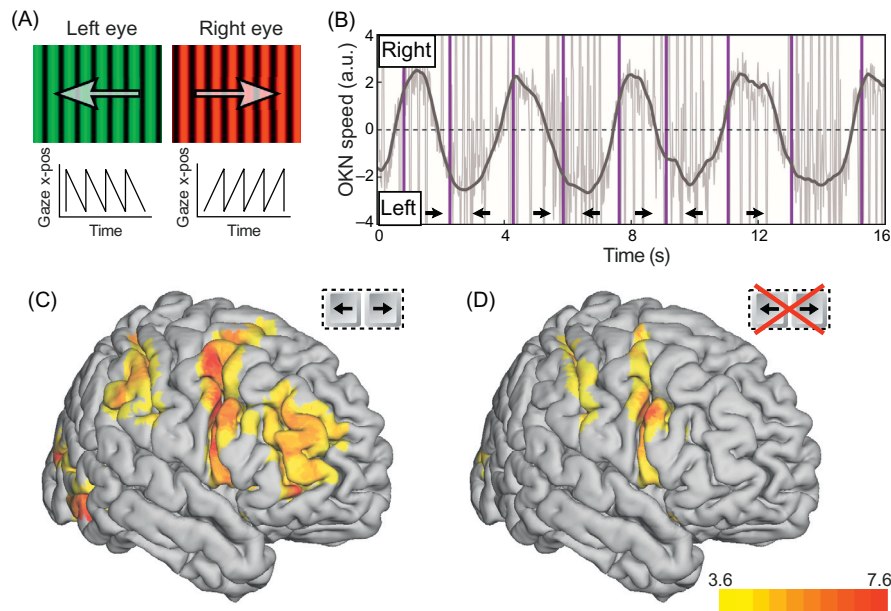


FIGURE 5.3 A no-report paradigm applied to binocular rivalry. (A) Green, leftward moving and red, rightward moving gratings were presented to the left and right eyes, respectively. This not only induces vigorous binocular rivalry between the two stimuli but also an optokinetic nystagmus (OKN), with characteristic slow and fast phase eye movements (Enoksson, 1963; Fox et al., 1975). (B) The speed of the OKN's slow phase (thick gray lines) can be used to infer the perceptual state of subjects (arrows at the bottom), which nicely coincides with their perceptual reports signaled via button presses (purple vertical lines). That is, when the subject reports seeing a red and rightward moving grating, both eyes execute the slow phase of the OKN to the right (see also Leopold et al., 1995). (C) and (D) fMRI BOLD contrasts at the time of perceptual transitions during rivalry compared with those during replay when subjects either (C) reported or (D) did not report their percept. Most of the right dorsolateral prefrontal cortex activation disappeared when subjects passively experienced rivalry without reports, implying that the right frontal activation is not a core neural correlate of consciousness (Aru et al., 2012; de Graaf et al., 2012) but may be a consequence of the need to report it. Source: Taken from Frässle et al. (2014).

consequences of consciousness, such as reports, working memory, and attention (Miller, 2007; Aru et al., 2012; de Graaf et al., 2012).

Another influential theory and model of consciousness is the global workspace theory of consciousness (Baars, 2005) and its elaboration into the global neuronal workspace (GNW) (Dehaene and Changeux, 2011). Dehaene and colleagues (2006) propose a tripartite ontology whereby any physical stimulus triggers either *subliminal*, *preconscious*, or *conscious processing*. What decides the fate of any stimulus is its strength and whether or not top-down attention is deployed. Their distinction maps onto ours if subliminal processing is equated with the upper and lower left quadrants and preconscious with the upper right quadrant. One important difference is our assumption that consciousness can occur without top-down attention (upper right quadrant in Table 5.1. Also see Cohen et al., 2012). Furthermore, the result of the above-mentioned no-report experiment of Frässle and colleagues (2014) challenges a central assumptions of GNW—that the central broadcasting that gives rise to conscious perception must always occur in prefrontal cortex.

Recently, Graziano and Kastner (2011) proposed that conscious awareness can be considered as a

perceptual reconstruction or model of attention, both of one's own as well as that of other people. It is a second-order representation of attention ("what am I looking at and what are other people looking at"). Their view on the relationship between attention and consciousness is left ambiguous¹ (see the commentaries in Koch, 2011).

OPTOGENETIC STUDIES TO ACHIEVE CONSCIOUSNESS WITH NO ATTENTION IN ANIMALS

How can we test if it is possible to perceive anything in the complete absence of top-down attention? No psychophysical manipulation may be effective in completely eliminating top-down selective attention (Cohen et al., 2012). A more radical alternative is to directly and mechanistically intervene into the brain to turn off top-down attention. Brain science has developed highly specific molecular tools to directly, transiently, reversibly but invasively manipulate the brain at the circuit level.

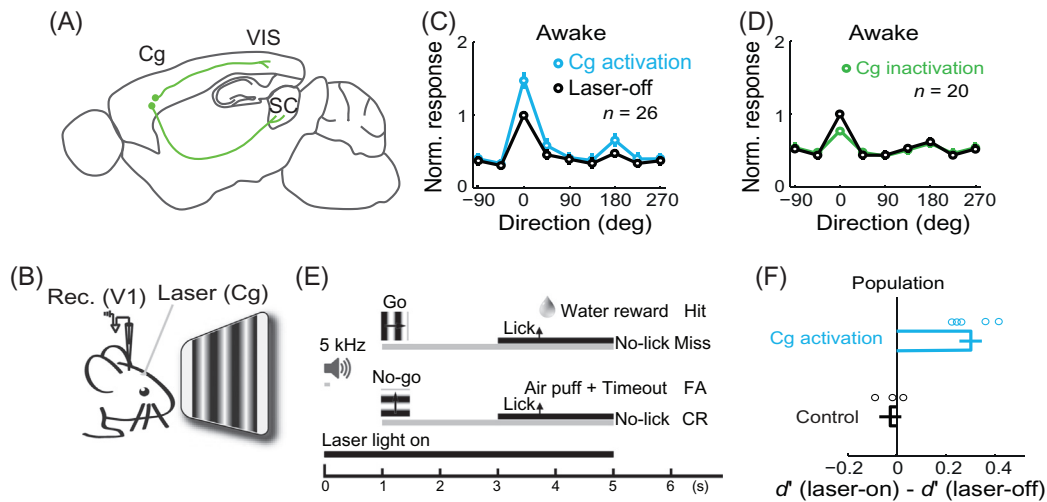


FIGURE 5.4 Optogenetic manipulation of top-down attention. (A) The cingulate cortex (Cg) in mice is anatomically and functionally homologous to the frontal eye field in primates, an important source of top-down spatial attention. (B) A genetically targeted subset of neurons in Cg, which directly project to the primary visual cortex (V1), can be selectively activated or inactivated by optogenetic tools, while neuronal activity can be simultaneously recorded from single neurons in V1. (C) and (D) Cg activation enhanced (C) and inactivation reduced (D) the orientation tuning of the V1 neurons. (E) In the behavioral task, mice performed a go/no-go orientation discrimination task by licking/no-licking a water tube (Lee et al., 2012). (F) The behavioral performance of orientation discrimination in these animals was enhanced by selective activation of the cingulate neurons. Such optogenetic techniques are becoming ever more precise in terms of their ability to intervene into the many tangled circuits of the central nervous system. Thus, it may soon be possible to experimentally block all top-down attentional modulation in such animals on a trial-to-trial basis and evaluate their behavior.

At present, the most powerful way to accomplish this is to rely on rapidly advancing optogenetic techniques in animals, especially in mice (Deisseroth, 2011; Yizhar et al., 2011) and to a lesser extent in monkeys (Han et al., 2009; Gerits et al., 2012; Diester et al., 2011). While experiments in animals pose their own challenges for consciousness research (Boly et al., 2013), techniques available for animal research is much more powerful than those available for human research. With the combined knowledge of cell-type specific brain-wide connectivity (Oh et al., 2014) and molecular promoters expressed by these neurons and their interconnections, it has become possible to transiently knock out the axons that project to early visual cortices from frontal and parietal areas as well as higher-order visual cortices. In the limit, one would obtain a purely feedforward set of cortical regions (with local inter-areal feedback) but no modulatory input from sub-granular layers in higher regions reaching down into superficial layers into earlier cortical or thalamic regions (Cruikshank et al., 2010).

Consider the experiment by Zhang and colleagues (2014). In primates, the neuronal source of top-down attentional amplification includes parts of frontoparietal cortex (Tsushima et al., 2006), such as FEF (Noudoost et al., 2010; Bressler et al., 2008). In mice, an

anatomical and functional homologue area is the cingulate cortex (Cg) (Figure 5.4A). Selective activation and inactivation of Cg neurons (Figure 5.4B) that project to the early visual areas (V1) enhanced or reduced orientation tuning of the V1 neurons (Figure 5.4C and D). Remarkably, Cg activation also enhanced behavioral performance of the mice (e.g., 0° vs 90° orientation discrimination in a go/no-go task, Figure 5.4E and F).

As is exemplified in the study by Zhang and colleagues, the extraordinary rapid development of ever more refined transgenic mice as well as viral techniques, both of which target specific, molecular and projectional defined neuronal populations that can be labeled, and turned on or off from anywhere from milliseconds to hours has given systems neuroscience an amazing ability to delicately, reversibly and transiently intervene and to observe the phenotype at the behavioral and at the circuit level (Huang and Zeng, 2013). The temporal precision of experimental control is better than 10 ms while the spatial one is limited by the size of the optical stimulation.

A major drawback of these molecular tools is their invasive nature, making them currently unsuitable for routine human use (although clinical trials for therapeutic intervention to alleviate retinal blindness in patients are being considered). Multi-focused ultrasound inactivation is a promising interventional technique that

is now being tested in patients in clinical trials to study the extent to which gray-matter volumes on the order of several mm can be safely and routinely activated or inactivated ([Legon et al., 2014](#); [Bystritsky et al., 2011](#); [Min et al., 2011](#); [Tyler et al., 2008](#); [Yoo et al., 2011](#)).

If top-down attention were to be completely, but transiently, inactivated by such a manipulation, the affected animal should be unable to perform a visual discrimination task if the target is presented together with distractors, whereas they would be able to perform the task at the normal, pre-intervention level if the target is presented without distraction. This would demonstrate that top-down attention would not be necessary for processing a single, isolated stimulus in an otherwise empty visual field. (Note in the above-mentioned study in mice, behavioral performance under Cg inactivation was not reported. It is also unclear if the visual orientation discrimination requires substantial amount of attention for mice such that it cannot be performed under the dual-task paradigm.)

To make sure that these tasks are performed consciously, the mice or monkeys could be trained to report their confidence via post-decision wagering ([Kepecs et al., 2008](#); [Kiani and Shadlen, 2009](#); [Persaud et al., 2007](#)). As the confidence or metacognitive judgment is likely to be mediated by medial orbito-frontal areas ([Fleming et al., 2010](#)) (but also see [Komura et al., 2013](#)), knocking out top-down attention in the cingulate cortex might not affect confidence judgment.

CONCLUDING REMARKS: 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, with little relevance to the real world. We believe otherwise.

A lasting insight into human behavior—eloquently articulated by Friedrich Nietzsche and, later on, by Sigmund Freud—is that much action bypasses conscious perception and introspection. In particular, [Goodale and Milner \(2004\)](#) isolated highly trained, automatic, stereotyped and fluid visuo-motor behaviors that function in the absence of phenomenal experience. As anybody who runs mountain trails, climbs, plays soccer, or drives home on automatic pilot knows, such sensory-motor skills—dubbed *zombie behaviors* ([Koch and Crick, 2001](#))—require rapid and sophisticated sensory processing. Confirming a long held belief among trainers, athletes performing their high-performance skills can do better under skill-irrelevant dual-tasks conditions (i.e., paying attention to tones) than when paying attention to their exhaustively

trained behaviors ([Beilock et al., 2002](#)). This also appears to be true for keyboard typing, something most of us are highly trained at ([Logan and Crump, 2009](#)).

The history of any scientific concept (e.g., energy, atom, gene) is one of increasing differentiation and sophistication until its essence can be explained in a quantitative and mechanistic manner in terms of elements operating at a lower, more elemental level. We are very far from this ideal in the inchoate science of consciousness. Yet functional considerations and the empirical and conceptual spadework of many early twenty-first century scholars make it clear that these psychologically defined concepts, top-down attention and consciousness, so often conflated, are not the same. One consequence of this distinction is that many of the neuronal correlates of consciousness that have been reported are probably confounded by the neuronal correlates of attention ([Macknik and Martinez-Conde, 2007](#); [Watanabe et al., 2011](#); [Koch and Tsuchiya, 2012](#); [Miller, 2007](#); [Aru et al., 2012](#); [de Graaf et al., 2012](#)). These empirical and functional considerations clear the deck for a concerted attack, employing powerful interventionalist tools in nonhuman animals or in people, on the core problem—that of identifying the necessary and sufficient neural causes of any one conscious percept.

QUESTIONS FOR FURTHER RESEARCH

1. How much of the quality 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? Specifically, how good are people at describing the gist of novel, natural scenes verbally under dual-tasks conditions ([Fei-Fei et al., 2007](#))? Can people give good metacognitive confidence judgment about the unattended aspects of the scene ([Kunimoto et al., 2001](#); [Kanai et al., 2010](#); [Persaud et al., 2007](#))? In most dual tasks, subjects are exposed to a lengthy training to stabilize the performance. Is conscious perception of gist without attention possible in untrained subjects ([Joseph et al., 1997](#); [Braun, 1998](#))?
2. Certain simple tasks (e.g., rotated L vs T, red/green vs green/red, [Figure 5.2](#)) seem impossible to perform even after extended period of training ([Fei-Fei et al., 2005](#)). Why? Are none of the aspects of these unattended stimuli perceived when attention is withdrawn? Or, are the elementary features or the global impression of these objects perceived? Is the positional relationship of elementary features difficult to perceive under poor attention? Can psychophysical and computational modeling of peripheral vision

- predict what aspects of the neuronal processing are affected by attention ([Freeman and Simoncelli, 2011](#); [Rosenholtz et al., 2012](#))?
3. What are the neuronal mechanisms that lead to improved zombie behaviors in the near absence of top-down attention ([Beilock et al., 2002](#); [Logan and Crump, 2009](#))? Do those aspects of reasoning, language processing and thinking that proceed in the absence of consciousness ([Jackendoff, 1996](#)) function better without top-down attention? What are the neuronal mechanisms where attention or consciousness interferes with the desired task performance?
 4. This review focuses on the selective amplification (and to a lesser extent inhibition) by top-down attention and its relationship to consciousness. Another potential role for top-down attention is to integrate information. While integration of information has been suspected to be the core of consciousness (for a review see [Mudrik et al., 2014](#)), the precise relation between integration, consciousness and attention is unclear. Many experiments have already established that a consciously perceived object can influence the processing of invisible objects, a form of integration of conscious and non-conscious perceived objects. Beyond such integration, recent studies demonstrate that integration of information between features within a natural photograph ([Mudrik et al., 2011](#)) and multiplication of two digits ([Garcia-Orza et al., 2009](#)) is possible even when the stimulus array itself remains perceptually invisible. What is the limit of non-conscious integration, in terms of spatial and temporal windows as well as cross modalities ([Mudrik et al., 2014](#); [Favre et al., 2014](#))? Does non-conscious information integration depend on top-down attention? Theoretically, what is the role of the top-down attention in the IIT of consciousness ([Tononi, 2004](#); [Oizumi et al., 2014](#))? What does the theory say about consciousness without attention, attention without consciousness, and the opposing effects of consciousness and attention?
 5. What are the effects of attention and consciousness during perceptual switches of multi-stable percepts? Some studies report that withdrawing top-down attention from ambiguous stimuli reduces the rate of perceptual switches ([Paffen et al., 2006](#); [Pastukhov and Braun, 2007](#)), while others claim that it completely abolishes binocular rivalry ([Zhang et al., 2011](#); [Brascamp and Blake, 2012](#)). With respect to consciousness, do perceptual switches occur even when the ambiguous stimulus itself is rendered invisible? When a left-going cloud of dots is presented to one eye and a right-going cloud to the

other eye, these dots alternate in conscious perception, a form of binocular rivalry. [Platonov and Goossens \(2014\)](#) found that when the luminance of the dots is lowered, subjects start to lose conscious sensation of visual motion in the display. Strikingly, however, subjects can still guess the direction of the motion, which exhibit typical properties of binocular rivalry; the strength of the stimulus on the left eye determines the dominance duration of the (guessed and invisible) stimulus on the right eye, and the detection threshold for a probe presented to the suppressed eye is higher than that to the dominant eye. Such binocular rivalry between invisible stimuli are consistent with two recent independent reports ([Dieter et al., 2013](#); [Zou et al., 2014](#)). Can such perceptual switching occur during loss of consciousness due to anesthesia ([Bahmani et al., 2014](#)) or sleep?

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NOTE

1. For instance, "Awareness, therefore, is not the same thing as attention, . . ." (p. 3) and "In the present hypothesis, therefore, the relationship between attention and awareness is rather complex" (ibid. p. 12).

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