Exploring Visual Attention Functions of the Human Extrageniculate Pathways Through Behavioral Cues

Raphaël Mizzi and George A. Michael
Université de Lyon, Université Lumière Lyon2

Over the past few decades, evidence has accumulated showing that, at subcortical levels, visual attention depends partly on the extrageniculate neural pathways, that is, those pathways that bypass the lateral geniculate nucleus and circumvent the primary visual cortex. Working in concert with neuroscience, experimental psychology has contributed considerably to the understanding of the role these pathways play through the use of 3 behavioral cues: nasal-temporal asymmetries, responses to S-cone stimuli, and responses to perceptually suppressed stimuli. In this article, after presenting the extrageniculate pathways and the role of each of the component structures in visual attention, we review findings from studies that have used these behavioral cues, as well as what they tell us about the role of the extrageniculate pathways in visual attention. We conclude that nasal-temporal asymmetries and responses to S-cone stimuli are plausible probes of extrageniculate functions, because they are consistent with neurophysiological, neuropsychological, and neuroimaging findings. By contrast, despite promising perspectives, the literature is yet too scarce for responses to perceptually suppressed stimuli to be considered as a plausible probe of extrageniculate-dependent attention functions.

Keywords: visual attention, extrageniculate, nasal-temporal, S-cone stimuli, perceptual suppression

The visual world is made of spatially distributed objects that, at any moment, may become relevant for behavior. The quantity of available information is such that it exceeds the processing capacity of the visual system. Visual attention then operates to prioritize a small portion of information for further detailed processing by orienting toward relevant locations, like a spotlight illuminating the garage. Selective attention to spatial locations can operate either automatically or involuntarily in response to signals coming from the visual field. In this case, it is referred to as exogenous attention. However, it can also be oriented voluntarily and in a controlled fashion when guided by internal states, aims and strategies. It is then referred to as endogenous attention. Even though exogenous and endogenous attention can be dissociated in the laboratory, they are rather functioning together in everyday situations. Furthermore, attention can be oriented in space either without any external signs that this has been done, that is, covertly, or with accompanying movements of the eyes, the head and even the whole body, that is, overtly. In summary, both exogenous and endogenous visual attention modulate the spatial and temporal

sensitivity of early perceptual filters, influence the selection of stimuli of interest (Carrasco, 2011). During the past 40 years, neurophysiology, neuropsychology, and neuroimaging have provided evidence that visual attention is controlled through largely distributed brain networks involving cortical and subcortical circuits (Bisley, 2011). At cortical levels, the parietal and the frontal lobes seem to be heavily involved in attention (Carrasco, 2011; Corbetta & Shulman, 2002, 2011; Posner & Petersen, 1990) and lesions to these lobes, especially in the right hemisphere, produce unilateral spatial neglect, one of the most dramatic neuropsychological deficits, causing failures to notice, attend to and process information in the contralateral visual field. At subcortical levels, research has focused on the thalamus and its interactions with cortical areas for producing controlled attentional modulatory effects (Ling, Pratte, & Tong, 2015; McAlonan, Cavanaugh, & Wurtz, 2008; O'Connor, Fukui, Pinsky, & Kastner, 2002; Purushothaman, Marion, Li, & Casagrande, 2012; Schneider, 2011). As far as automatic processes involved in attentional selection are concerned, research has mostly focused on neural pathways that convey information from the retina to the extrastriate cortices that bypass the lateral geniculate nucleus (LGN) of the thalamus and circumvent the primary visual cortex: the extrageniculate pathways (Knudsen, 2011; Krauzlis, Lovejoy, & Zénon, 2013; Lyon, Nassi, & Callaway, 2010; Robinson & McClurkin, 1989). It was suggested that the extrageniculate pathways operate to represent the location of important signals in space (Krauzlis, Liston, & Carello, 2004; Krauzlis et al., 2013; Saalmann & Kastner, 2011; Wurtz, McAlonan, Cavanaugh, & Berman, 2011). This is not just a perceptual function; it is a specific primitive attentional function that separates important locations from secondary ones and, therefore, confers selection and processing priority.

In primates, the extrageniculate pathways are phylogenetically older visual systems. Retinal ganglion cells project to at least two

This article was published Online First October 10, 2016.

Raphaël Mizzi and George A. Michael, EMC Laboratory, Department of Cognitive Psychology and Neuropsychology, Université de Lyon, Université Lumière Lyon2.

This work was supported by the LABEX CORTEX (ANR-11-LABX-0042) of Université de Lyon, part of the "Investissements d'Avenir" program (ANR-11-IDEX-0007) run by the French National Research Agency (ANR).

Correspondence concerning this article should be addressed to Raphaël Mizzi, EMC Laboratory, Department of Cognitive Psychology and Neuropsychology, Université Lumière Lyon2, 5 avenue P. Mendès-France, 69676 Bron Cedex, France. E-mail: raphael.mizzi@univ-lyon2.fr

structures outside the lateral geniculate nucleus (see Figure 1). The first target is the superior colliculus (SC), more precisely its superficial layers (Pollack & Hickey, 1979). This retino-tectal pathway reaches the cerebral cortex through the pulvinar nucleus of the thalamus (Berman & Wurtz, 2010; Harting, Huerta, Frankfurt, Strominger, & Royce, 1980; Lyon et al., 2010). The second target of retinal cells is the pulvinar itself. Retinofugal fibers end up in the inferior, lateral, and medial parts of the pulvinar (Itaya & Van Hoesen, 1983; Mizuno, Itoh, Uchida, Uemura-Sumi, & Matsushima, 1982; Nakagawa & Tanaka, 1984; O'Brien, Abel, & Olavarria, 2001) and this constitutes the direct retino-pulvinate pathway. Signals in the peripheral visual fields activate extra-

geniculate pathways seemingly to trigger the oculomotor and attentional systems. Indeed, neurons in the superficial layers of the SC show an enhanced response to the presence of a stimulus that serves as the target of a saccadic eye movement even in the absence of any saccade (Goldberg & Wurtz, 1972). The primate SC may contribute to visual attention by providing the signal for its shifts through space and by facilitating saccades and head movements toward relevant locations of the visual field (Kato, Takaura, Ikeda, Yoshida, & Isa, 2011; Krauzlis et al., 2004). Recent investigations have backed up this hypothesis by showing that the SC plays a central role in the control of spatial attention and the process of target selection (Krauzlis et al., 2013; Shen,

Figure 1. Illustration of the retinal projections reaching the extrastriate cortices that bypass the lateral geniculate nucleus and the primary visual cortex. Are represented the pathways supposed to be involved in the techniques reviewed. Information from temporal visual fields are more represented in contralateral extrageniculate structures (hatched vs. plain VF and pathways). Information from all types of ganglion cells are transmitted through the geniculate pathway, while no information from beta ganglion cells is transmitted to the superior colliculus.

Valero, Day, & Paré, 2011). The role of the pulvinar in attention is less clear. Neurophysiological recordings conducted on primates and neuroimaging in humans have shown that portions of the pulvinar exhibit attention-related activity (Buchsbbaum et al., 2006; Fischer & Whitney, 2012; Petersen, Robinson, & Morris, 1987; Strumpf et al., 2013), and dysfunction of the pulvinar in both monkeys and humans produces deficits in visual attention (Arend et al., 2008; Michael, Boucart, Degreef, & Godefroy, 2001; Michael & Desmedt, 2004; Rafal, Inhoff, Friedman, & Bernstein, 1987; Snow, Allen, Rafal, & Humphreys, 2009). Some of the attention-related activity in the pulvinar seemingly originates in the SC and might contribute to modulation and enhancement of neuronal response in cortical areas (Saalmann & Kastner, 2011; Wurtz et al., 2011). This is, for example, supported by evidence that pulvinar neurons with input from the SC have properties that are similar to those of neurons in the superficial layers of the SC in that they have visual but not presaccadic activity (Berman & Wurtz, 2008). Yet, in view of the direct retinal input it receives (Itaya & Van Hoesen, 1983; Nakagawa & Tanaka, 1984; O'Brien et al., 2001), the pulvinar can be hardly considered as just a passive relay of information that was previously processed by the SC.

In view of the numerous connections that exist between subcortical and cortical areas that are critical to attention (Bisley, 2011; Wurtz et al., 2011), it is of the utmost interest to unravel the role of whole pathways in attention, rather than the respective role of each specific brain structure of these pathways (Leopold, 2012). For instance, key structures for the expression of attention, such as the occipito-temporal, lateral intraparietal areas and the inferior parietal lobule (Fecteau & Munoz, 2006; Kusunoki, Gottlieb, & Goldberg, 2000; LaBerge, 2002) receive afferents from both the geniculate and the extrageniculate pathways (Baizer, Desimone, & Ungerleider, 1993; Chambers, Payne, Stokes, & Mattingley, 2004; Clower, West, Lynch, & Strick, 2001). This sketches the scenario that signals that are used to guide attention are built on combined geniculate and extrageniculate inputs. However, given the different anatomical and functional properties of neurons of these pathways, it is naturally expected that their respective contributions be different and probably complementary (Schneider & Kastner, 2009). The idea of a complementarity between the two pathways in attention functions is backed up by the fact that, in primates, the older extrageniculate pathways did not disappear with the evolution of the more recent and more dominant geniculate pathway but, instead, increased in volume (Rao & Wu, 2001). For instance, differences in the speed with which signals are conveyed through these pathways toward cortical areas subtending attention have already been hypothesized (Chambers et al., 2004), as well as differences in the quantity and quality of the signals conveyed (Michael & Desmedt, 2004; Michael & Gálvez-García, 2011; Mizzi & Michael, 2014). Stimulating each of these two pathways with the same stimulus should therefore provide evidence of how they contribute to directing attention. In an attempt to understand the role of these pathways and complement knowledge coming from neurophysiology, neuropsychology, and neuroimaging, experimental psychologists have considered behavioral cues as reflecting functional differences between the geniculate and the extrageniculate pathways. It has to be pointed out that these effects cannot directly attest to the extrageniculate involvement because of their behavioral nature, and several arguments that run counter have been given. Nevertheless, these effects are generally inter-

preted in terms of extrageniculate modulation, be it oculomotor or attentional, because of some specificities of the visual system that will be mentioned later on. Three of those cues are reviewed here: (a) asymmetric responses to stimuli presented in the nasal and the temporal visual fields, (b) responses to short-wavelength stimuli (S-cone stimuli), and (c) responses to perceptually suppressed stimuli. Each cue is taken individually and examined closely.

Nasal-Temporal Asymmetries

Neurophysiologists have noted that direct retinal input to the monkey SC and pulvinar is strongly contralateral (Goldberg & Wurtz, 1972; Hendrickson, Wilson, & Toyne, 1970; Hubel, LeVay, & Wiesel, 1975; Itaya & Van Hoesen, 1983; Wilson & Toyne, 1970) and conveys information from the contralateral visual field up to the visual extrastriate cortices (see Figure 1; Adams, Hof, Gattass, Webster, & Ungerleider, 2000; Berman & Wurtz, 2008, 2010, 2011; Lyon et al., 2010). For instance, small retinal lesions that are followed by degeneration of nerve fibers have revealed that retino-tectal projections are denser in the contralateral than in the ipsilateral SC (Wilson & Toyne, 1970; Figure 2). Similarly, tract-tracing techniques have revealed that the retina has denser direct projections to the contralateral than to the ipsilateral inferior pulvinar (Itaya & Van Hoesen, 1983; Mizuno et al., 1982). Imaging techniques have revealed that, in humans, the SC and the pulvinar respond strongly, if not exclusively, to contralateral visual stimuli (Cotton & Smith, 2007; Schneider & Kastner, 2005). This means that, despite the whole visual field being represented in the SC and the pulvinar, input from the temporal visual field (the left side for the left eye and the right side for the right eye) could be mostly processed by the contralateral SC and pulvinar than input from the nasal visual field (the left side for the right eye and vice versa).

The relevance of this kind of asymmetry in behavior has been demonstrated in humans. Because fibers that carry information from the nasal field mature more slowly than fibers that carry information from the temporal field to the SC, it could be expected that newborns, in whom the retino-tectal pathway is thought to

Figure 2. The degeneration of nerve fibers after small retinal lesions of the left eye in primates reveal that retinal projections are more dense in the contralateral than in the ipsilateral superior colliculus (modified from Wilson & Toyne, 1970). "X" symbols represent degenerated fibers, more numerous in the contralateral superior colliculus.

mature before the geniculate pathway (Johnson, 1990), gaze more accurately at stimuli in the temporal field (Rothbart, Posner, & Boylan, 1990). Lewis and colleagues (Lewis, Maurer, & Blackburn, 1985) compared infants' ability to detect-by-gaze stimuli of varying sizes in the nasal and temporal fields. They found that detection in the temporal field was better than detection in the nasal field. In fact, the smallest stimuli detected by 1-month-old infants in the temporal field were more than eight times smaller than those detected in the nasal field. This finding complemented earlier reports that infants scanning stimuli monocularly tend to look longer at the temporal side of a figure than at the nasal side (Slater & Findlay, 1972).

Along with the neurophysiological studies in monkeys mentioned earlier, such observations led researchers from the field of the psychology of attention to speculate that, under monocular viewing conditions, functions that heavily depend on the SC (Rafal, Machado, & Ingle, 2000), such as the control of reflexive eye movements, would be dominated by stimuli presented in the temporal field (Posner & Cohen, 1980). The logic was that information from the temporal field would be conveyed faster through extrageniculate pathways toward the extrastriate areas, and their activation would have different effects on saccadic eye movements than information from the nasal field. Nasal-temporal asymmetries could hence be considered as a marker that could help differentiate the functions of the geniculate and the extrageniculate pathways. Such asymmetries may be less pronounced in human adults and are influenced by physiological asymmetries. For instance, physiological studies have shown a greater density of photoreceptors (Osterberg, 1935) and ganglion cells in the nasal retina which processes information from the temporal visual field (Curcio & Allen, 1990). In agreement, psychophysical studies have shown higher luminance thresholds and lower acuity in the nasal visual field (Fahle & Schmid, 1988). Accordingly, attentional-related asymmetries could still be detectable with subtle behavioral measures. In one of their experiments, Posner and Cohen (1980) briefly presented one dot in the nasal field and another one in the temporal field of participants who had been instructed to move their eyes to whichever dot they wanted. In a condition where one dot preceded the other in time, participants naturally gazed at the dot that appeared first. However, in a condition where the dots were presented simultaneously, participants generally gazed at the dot presented in the temporal field. This result was replicated later on (Shulman, 1984). When it comes to comparing automatic versus controlled saccadic parameters, research has not always yielded equivocal results because differences for the nasal and temporal fields have not always been found (Honda, 2002; Jóhannesson, Asgeirsson, & Kristjánsson, 2012). This topic is still under debate as, according to the abovementioned hypothesis, extrageniculate signals would be conveyed faster and would probably trigger faster oculomotor responses. Yet, no clear and direct evidence on such a temporal asynchrony between the geniculate and the extrageniculate pathways has been provided so far. Those results contrast with the idea that all oculomotor parameters constantly show nasal-temporal asymmetries, and they have, therefore, led some authors to contest the extrageniculate mediation of such effects. For instance, Jóhannesson and colleagues (2012) advanced that, since the retino-tectal pathway is formed by only about 10% of ganglion cell projections (Perry & Cowey, 1984), its contralateral implication in saccadic latencies would be minor. Notwithstanding, some

physiological studies have shown that collicular oculomotor activity is influenced by descending projections from cortical structures (Fries, 1984; Gaymard, Lynch, Ploner, Condy, & Rivaud-Péchoux, 2003; Machado & Rafal, 2004a; Ploner, Gaymard, Rivaud-Péchoux, & Pierrot-Deseilligny, 2005; Sommer & Wurtz, 2000; Wilson & Toyne, 1970). For instance, Rafal (Rafal, 2006) showed that lesions of the frontal eye fields (FEF) lead to contralateral disinhibition of involuntary saccades and the impairment of involuntary ipsilateral saccades. These results, confirmed through electrical and transcranial magnetic stimulation techniques (Burman & Bruce, 1997; Müri et al., 1998), demonstrated the importance of the fronto-tectal pathway in the control of involuntary saccades.

On the other hand, peak velocities of saccadic eye movements (i.e., the highest velocity that the eye reaches during a saccade) under monocular viewing conditions are higher toward temporal than toward nasal stimuli (Jóhannesson & Kristjánsson, 2013). This effect cannot be accounted for by differences in saccade amplitude between the fields. In another study, Walker and colleagues (Walker, Mannan, Maurer, Pambakian, & Kennard, 2000) required participants to make an eye movement toward a pre-defined target and ignore any other irrelevant stimuli presented in the visual field. They reported stronger oculomotor distraction effects when the irrelevant stimuli were presented in the temporal field than in the nasal field. Similarly, Rafal and colleagues (Rafal, Smith, Krantz, Cohen, & Brennan, 1990) reported that irrelevant distracting stimuli presented in the blind field of patients having suffered damage to the visual cortex inhibited saccades toward target stimuli presented in the intact part of their visual field. But this effect was observed only when the distracting stimuli were presented in the temporal field. While those reports concerned prosaccades, that is eye movements from the currently fixated location directly to the location of a stimulus appearing at the periphery of the visual field, other investigations found nasal-temporal asymmetries in antisaccades. Antisaccades are voluntary eye movements in the opposite direction to the location of a peripheral stimulus that require overcoming the natural tendency to move the eyes toward that stimulus. This is done through modulation of the activity of the SC by cortical areas such as the frontal eye fields (Everling & Fischer, 1998). Kristjánsson and colleagues (Kristjánsson, Vandenbroucke, & Driver, 2004) found that it was more difficult to overcome a prosaccadic tendency for a stimulus presented in the temporal field, supporting that stimuli occurring there exert a stronger oculomotor attraction.

Nasal-temporal asymmetries were first considered to concern only oculomotor processes (Posner & Cohen, 1980; Rafal et al., 1990; Shulman, 1984). However, the close relationship between saccadic eye movements and attention (Kustov & Robinson, 1996; Rizzolatti, Riggio, Dascola, & Umiltà, 1987) and the hypothesis that both the SC and the pulvinar are involved in attention (Krauzlis et al., 2013; Kristjánsson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007; Petersen et al., 1987; Posner, Cohen, & Rafal, 1982; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Robinson & Petersen, 1992) pushed researchers to look out for such asymmetries in tasks of spatial attention too. Evidence was obtained from several attention paradigms in which manual responses or perceptual judgments were required. For instance, in one study on orienting of attention in space (Rafal, Henik, & Smith, 1991), participants were required to detect a peripheral target by making either an eye movement to it, or by pressing manually a response

button while keeping the eyes on a central fixation stimulus. To summon attention, the target was preceded by a cue, which could appear at the location of the target or elsewhere (spatial cueing paradigm). A temporal field advantage was observed for both saccades and manual response times. Similar effects were observed in the accuracy of perceptual judgments (Ansorge, 2003), and were extended to other elementary operations of spatial attention such as inhibition of return (IOR; Berger & Henik, 2000). These findings suggest that nasal-temporal asymmetries are not exclusively related to oculomotor behavior, but are also related to attention. There is also evidence on attention effects that parallels the finding that temporal field stimuli have stronger inhibitory effects on eye movements (Walker et al., 2000) and exert a stronger prosaccadic tendency that is more difficult to overcome (Kristjánsson et al., 2004): responding manually to a target that appears above or below fixation is more affected and slowed down by attention-capturing distractors that appear in the temporal field (Michael & Buron, 2005). On the other hand, Zackon and colleagues (Zackon, Casson, Zafar, Stelmach, & Racette, 1999) used a temporal order judgment paradigm. Participants were required to judge which one of two laterally and simultaneously presented stimuli appeared first. In some cases, a spatial cue preceded the appearance of the stimuli at varying time intervals, drawing attention toward one field or the other. The authors found that participants perceived the stimulus in the temporal field as having appeared first, suggesting that the effect of attention was stronger when the cues were presented in the temporal field. Similar results were obtained with the split priming motion induction paradigm (Zackon, Casson, Stelmach, Faubert, & Racette, 1997). Here, two asynchronous lateralized spatial cues were followed by the appearance of a horizontal bar. Because of the attentional effect triggered by the cues, the bar seemed to move progressively from the two lateral cues toward a central collision point, which was the fixation point. If attention were more attracted to one field than the other, then the perception of motion would be perceived as faster. The authors reported that when the first cue appeared in the temporal field, the perceived collision point was closer to fixation than when the first cue appeared in the nasal field, suggesting a temporal advantage for attention.

Even though neurophysiological data suggests that both the SC and the pulvinar may also be involved in the selection of targets when presented on a background of irrelevant distractors (Buchsbaum et al., 2006; Fischer & Whitney, 2012; Knudsen, 2011; Lovejoy & Krauzlis, 2010; Rotshtein, Soto, Grecucci, Geng, & Humphreys, 2011; Strumpf et al., 2013), little has been done to investigate nasal-temporal asymmetries in tasks that require to find and select a target among distractors. And when attempts were made, such asymmetries proved difficult to obtain. This is consistent with neuropsychological results that in some cases showed deficits in resolving competition among visual stimuli after lesions of the pulvinar in humans (Snow et al., 2009) and sometimes did not show such deficits. For instance, Michael and Ojeda (2005) presented healthy participants with a lateralized tachistoscopic visual search task in which a target was presented among four task-irrelevant distractors. The target-distractor physical similarity varied parametrically to manipulate attention demands. While asymmetries were obtained for left versus right visual fields as a function of attention demands under binocular viewing conditions, no

asymmetries between nasal and temporal displays under monocular viewing conditions were found. However, in another investigation on the way attention progresses without eye movements on the basis of items' visual salience in a search display containing one target and two distractors, a nasal-temporal asymmetry was found (Michael & Gálvez-García, 2011). Attention progresses from the most toward the least salient item until a target is found. This makes responses slow down and accuracy shrink almost linearly with decreasing visual salience of the target. Consequently, the shallower the slope of such a change, the more the shifting from the most toward the least salient item is facilitated. The authors observed a well-marked nasal-temporal asymmetry in accuracy, but only when the stimuli were projected to the temporal field of the left eye and the nasal field of the right eye, both projecting to the right hemisphere. These two hemifields carry information toward the right cerebral hemisphere. The authors consequently interpreted this asymmetry as mainly involving the right hemisphere (see Figure 3). This is in agreement with hypotheses and findings that the right hemisphere is specialized in attentional processes at both cortical and subcortical levels (Carrasco, 2011; Corbetta & Shulman, 2002; Habekost & Rostrup, 2006; Karnath, Himmelbach, & Rorden, 2002; Kingstone, Friesen, & Gazzaniga, 2000). Compared with displays presented in the nasal field, performance slopes were six times smaller for

Figure 3. Accuracy slopes in the nasal and temporal fields in a modified task of visual search. Attention progresses from the most salient to the least salient item of a scene until the target is found, making accuracy to decrease with decreasing salience of the target. The smaller the slope of such a change, the more the shifting from the most toward the least salient item is easy and efficient. Note that the smallest slope is in the temporal field projecting to the right hemisphere (from Michael & Gálvez-García, 2011).

temporal field displays. This means that the progression of attention from the most salient toward the least salient item of the display is easier and more efficient in the temporal field. Furthermore, this nasal-temporal asymmetry was quite regular because it was found in the performance of 87.5% of participants. A similar observation has been made in a more recent study from our laboratory that specifically targeted filtering out distractors (Michael, Mizzi, Couffe, Gálvez-García, & Labeye, 2016). Participants viewed briefly presented sets of four similar stimuli among which a target could be present or not. The spatial organization of those sets was such that the need for attentional filtering was either low or high. A temporal field advantage was found only in conditions where the need for filtering was high, and only for stimuli presented to the right hemisphere. To our knowledge, these are the only studies that reported nasal-temporal asymmetries in tasks that involved selecting a target among multiple distractors. Therefore, it is difficult, on the basis of the extant behavioral studies, to draw strong conclusions on the respective contribution of the geniculate and extrageniculate pathways in filtering out distracting signals. This is mostly because, to our knowledge, only three such studies on healthy participants have been published.

All the abovementioned findings suggest that there is a difference in performance when people have to process and respond to signals occurring in the temporal field as compared with those appearing in the nasal field. The problem is that the ultimate validity of the hypothesis postulating a numerical superiority of projections from the temporal field to extrageniculate targets is controversial. Williams and colleagues (Williams, Azzopardi, & Cowey, 1995) objected that studies pointing asymmetrical projections from the nasal and temporal fields to the SC made this observation qualitatively, following anterograde transport of tritiated amino acids from the eye in monkeys. We may also add here that retinal lesion studies (Wilson & Toyne, 1970) also provide indirect evidence, since what is investigated is the density of the subsequent degeneration in the SC. A quantification of the retinal projections to the SC would provide stronger support to the temporal field numerical superiority hypothesis. In their study on four *Macaca mulatta* monkeys, Williams and colleagues (Williams et al., 1995) compared the average nasal/temporal ratio of the vast majority of retinal cells projecting to the midbrain to the nasal/temporal ratio of a standard retina. They found no evidence that retinal projections from the temporal field were more numerous than those from the nasal field. This finding matched an earlier investigation that had also failed to find any numerical superiority of retinal projections coming from the temporal field (Perry & Cowey, 1984). The authors consequently concluded that “there is nothing numerically anomalous about the projection to the midbrain” (p. 585). However, such a negative result calls for caution since the absence of evidence on numerical nasal-temporal asymmetries is not evidence of its absence. The apparent absence of numerical superiority in the projections of the retina to the SC does not preclude the possibility that the same projections are differently distributed when compared with retinal projections to the LGN. As far as the direct retino-pulvinar pathway is concerned, there is much less controversy because there is reliable evidence of a numerical superiority of projections coming from the temporal visual field (Itaya & Van

Hoesen, 1983). What about humans? Neuroimaging techniques showed that the temporal field is indeed overrepresented in the human contralateral SC, whereas such asymmetry is not found in the LGN and V1 (Sylvester, Josephs, Driver, & Rees, 2007). Furthermore, lesions of the SC and the pulvinar in humans abolish nasal-temporal asymmetries (Sapir, Rafal, & Henik, 2002; Sapir, Soroker, Berger, & Henik, 1999).

S-Cones Stimuli

Photopic vision, which provides high acuity in detection of light and color stimuli, is supported by three families of retinal photoreceptor rod cells named after their wavelength sensibility: L-cone (for large), M-cone (medium), and S-cone (short) wavelength. Luminance is coded by L- and M-cones and color coding requires all three cell families. Visual information is transmitted to three ganglion cell classes: α , β , and γ , which are involved in the processing of distinct visual dimensions (Rodieck & Watanabe, 1993; Wässle & Boycott, 1991). Alpha cells, mostly parasol ganglion cells, carry information to the magnocellular layers of the LGN as well as in the SC and are involved in contrast and luminance perception. Beta cells, mostly midget cells, transmit information only to the parvocellular layers of the LGN but not to the SC (see Figure 1). They carry color information and are responsible for fine perception. Gamma cells (only 10% of ganglion cells) possess various characteristics and are thought to play a role in global light or motion orientation detection, but they are colorblind. Gamma cells transmit visual information to both the LGN and the SC. While the retino-tectal pathway conveys both L- and M-cone information, numerous physiological studies (de Monasterio, 1978; Marrocco & Li, 1977; Schiller & Malpeli, 1977) have shown that there is no—or very sparse—information transfer from the S-cone cells to the SC. Indeed, the SC does not receive any projection from β ganglion cells. Thus, retino-tectal fibers do not convey short wavelength signals (de Monasterio, 1978; Marrocco & Li, 1977; Schiller & Malpeli, 1977), leaving the SC colorblind. The relevance of this kind of observation in humans was demonstrated by Tamietto and colleagues (Tamietto et al., 2010) using functional magnetic resonance imaging (fMRI). The authors showed that the human SC is selectively insensitive to S-cone stimuli. Consequently, presenting S-cone stimuli that are only detectable by the geniculate pathway and to which the retino-tectal pathway is blind allows the production of temporary, noninvasive and entirely reversible lesion-type effects in healthy humans. This can help assess behavior in the absence of retino-tectal processing (Calkins, 2001; Smithson, 2014; Sumner, Adamjee, & Mollon, 2002).

Isolating the precise color transition that only activates S-cones of the retina requires a specific methodology. S-Cone stimuli consist of a color transition that activates exclusively shortwave retinal rods. Shortwave receptors are classically known to be specialized in blue color perception, responding to a transition from gray to lilac-blue, or 0° of theoretical angle in the MacLeod-Boynton color coordinate (MacLeod & Boynton, 1979). However, they can also be found in literature as pink on a standard gray background. In fact, the color angle is slightly rotated from lilac-blue to pink when presenting stimuli in parafoveal locations because of diminishing macular pigmen-

tation (Calkins, 2001; Smithson, 2014).¹ Several methods are possible when selecting the specific color transition that would only solicit S-cone activity among isoluminant color candidates (Smithson, 2014; Smithson, Bourke, Zaidi, Mollon, & Stockman, 2004): the Webster method (Webster & Mollon, 1994), the minimally distinct border method (Boynton & Kaiser, 1978), and the transient trianopia procedure (Smithson, Sumner, & Mollon, 2003). These methods are used to assess the tritan line, which is the axis of color space that modulates only the excitation of the S-cones. The most recent procedure (Smithson et al., 2003) is based on a temporal desensitization of the blue-receptive cells, resulting in a temporary trianopia (Mollon & Polden, 1975). Participants are asked to detect a candidate color item while the S-cone cells are made insensitive. A transient desensitization is produced with a homogeneous yellow screen presentation (580 nm) before a detection task of the color candidates. The color transition for the candidate that elicits the lowest performance is the most affected by S-cones desensitization. Thus this candidate, which is specific to each participant, is used for subsequent behavioral testing.

The few studies that have used the S-cone isolation technique have been conducted to assess the implication of the SC in blind-sight (Leh, Mullen, & Ptito, 2006; Leh, Ptito, Schönwiesner, Chakravarty, & Mullen, 2010; Tamietto et al., 2010), in the attentional modulation of the responses of the occipital cortex (Wang & Wade, 2011), or in spatial attention (Bompas, Sterling, Rafal, & Sumner, 2008; Bompas & Sumner, 2009; Mizzi & Michael, 2014; Sumner et al., 2002; Sumner, Nachev, Castor-Perry, Isenman, & Kennard, 2006; Sumner, Nachev, Vora, Husain, & Kennard, 2004). The findings of this new field of research have shed some light on and modified our view on the attention functions of the retino-tectal pathway. Contrasting with previous investigations, the results of a series of studies from Sumner and colleagues (Bompas et al., 2008; Bompas & Sumner, 2009; Sumner et al., 2002, 2004, 2006) showed that the retino-tectal pathway does not underlie all attention functions that have been attributed to it in the past, such as exogenous orienting and IOR. In one well-constructed investigation, the authors conducted two distinct experiments in which participants were asked to react to the appearance of a lateral luminance target. In the first experiment, the authors assessed the oculomotor distractor effect. Participants were asked to gaze toward the target and to ignore an S-cone distractor appearing at the same time in the opposite visual field. In the second experiment, to assess shifts of spatial attention, participants had to detect the target with a button release. The target could appear at the location of a previous S-cone spatial cue. The results showed that the use of S-cone stimuli suppressed any oculomotor distractor effect, but did not prevent spatial shifts of attention. In a subsequent publication (Sumner et al., 2004), they also differentiated the attentional IOR effect from the saccadic IOR effect by showing that the first was not affected by the use of S-cone stimuli, while the latter was. Similar results were observed by Bompas and colleagues (Bompas et al., 2008; Bompas & Sumner, 2009). The findings of these studies initially suggested that the retino-tectal pathway was not necessary for shifts of attention through space, but was essential for oculomotor functions. However, these results are in contradiction with most of the extant literature that suggests that the retino-tectal pathway is involved in covert spatial shifts of attention. In a more recent study, Mizzi and Michael (2014) have

investigated the impact of S-cone stimuli on the salience-based progression of attention in a tachistoscopic visual search task without eye movements. The display could contain either luminance or S-cone stimuli and involved a target among two distractors of various saliences. In agreement with the findings of Sumner and colleagues (Sumner et al., 2002, 2004), the authors showed that the use of S-cone stimuli did not prevent initial attentional capture by the most salient item. Yet, contrary to what was observed with luminance stimuli, the subsequent progression of attention from the most salient item to the next one and so on (Michael & Gálvez-García, 2011) was completely suppressed. These findings suggest that, for attention to progress through space in search of the target, the retino-tectal pathway is necessary, even though no eye movements are required (Himmelbach, Erb, & Karnath, 2007).

Studies that have assessed the extrageniculate functions on the basis of the S-cone isolation technique have compared performance obtained with luminance stimuli to that obtained with S-cone stimuli. Still, a central question is rarely discussed in the conclusions of these studies: are those stimuli comparable (Calkins, 2001; Hendry & Reid, 2000)? In fact, the visual system is approximately four times less sensitive to S-cone stimuli (Wyszecki & Stiles, 1982). Some authors, therefore, arbitrarily increased the size of the S-cone items to render stimuli “comparable” (Sumner et al., 2004), while others kept all sizes strictly identical (Mizzi & Michael, 2014). The blue-sensitive system is also different in terms of transmission speed and is qualified as sluggish (Smithson & Mollon, 2004; Stockman, MacLeod, & DePriest, 1991; Stockman, MacLeod, & Lebrun, 1993). Here again, not every S-cone experimental investigation took into account this specificity in the interpretation of the results. These discrepancies create difficulties when it comes to comparing the results between different studies. Another limit comes from a recent report by Hall and Colby (2014). The authors challenged the hypothesis that S-cone stimuli would leave the retino-tectal pathway blind to the visual information. They recorded activation of neurons in the SC for S-cone stimuli in Old World monkeys. Therefore, they postulated that such observations would rule out any conclusion made upon the retino-tectal functions on the basis of the S-cone isolation technique. Nevertheless, Hall and Colby’s study failed to distinguish whether the activation of the SC recorded after presentation of S-cone stimuli arose from a direct

¹ This specific color transition that does not stimulate large and medium rod cells differs between individuals and between retinal locations because of retinal sensitivity, macular pigmentation, lens density, and chromatic aberration variations. Therefore, to determine the specific S-cone color transition for each participant, S-cone stimuli have to be individually calibrated by means of independent pilot protocols. This specific color transition requires the use of isoluminant stimuli. Classically, a set of color variations (i.e., the candidates) is compared to the background color to adjust, for each participant, the correct color variation. To this aim, the Minimum Motion Technique (Anstis & Cavanagh, 1983) is of much use. Here, a square-wave grating of red and green bars of spatial frequency 2.5 cycle deg⁻¹ is presented on the screen. This display flickers at a rate of 4 Hz with alternating dark and light stripes of the same width, interleaved in a four-stroke cycle. From this flickering emerges an optical illusion: vertical bars seem to move from left to right when the candidate color is brighter than the background color and from right to left when it is darker. When no motion illusion is perceived, the presented color variations are considered to be isoluminant.

retinal input, in which case their allegations would be correct, or from a cortical projection. This leaves open the possibility of a retro-activation of the SC from cortical areas, which would probably take place later on in the course of visual processing (Hall & Colby, 2014; Mizzi & Michael, 2014). In this case, such activation would not concern the retino-tectal pathway itself. Indeed, it has never been postulated that the SC would not (at some point) process the information conveyed through S-cone signals, but only that S-cone stimuli would prevent signals from the retina from reaching the SC directly. Thus, until neurophysiological studies provide more precise information about the way S-cone stimuli are processed by the SC, the conclusions of the abovementioned literature about the role of the extrageniculate pathways in attention functions are still valid.

Perceptually Suppressed Stimuli

In the 1950's, Denny-Brown and Chambers (1955) reported that after bilateral ablation of the striate cortex that produced total cortical blindness in monkeys, the animals were still able to locate moving objects, even under conditions of low luminance. The effects of damage to the striate cortex are very similar in monkeys and humans (Stoerig & Cowey, 1997). Interestingly though, cortically blind humans report not being aware of their capacity to guide their behavior visually, a condition that was termed blindsight (Weiskrantz, 1986). Blindsight was considered "alike a spotlight on the nature of unconscious or covert awareness" (Cowey & Stoerig, 1991). Subsequent research suggested that some oculomotor and attention functions may still be preserved in the blind field of patients with blindsight, such as the oculomotor distractor effect (Kentridge, 2012; Kentridge, Heywood, & Weiskrantz, 1999; Rafal et al., 1990; Yoshida et al., 2012). However, the neural circuitry underlying blindsight caused much ink to flow (Cowey, 2010; Leh, Johansen-Berg, & Ptito, 2006; Leopold, 2012; Overgaard, 2012; Weiskrantz, 2009). It has been pointed out that a difficult and frustrating feature of blindsight is that the evidence fails to converge on a single pathway among the several that bypass the primary visual cortex. For instance, it has been suggested that blindsight is supported by at least one pathway that involves the LGN (Cowey, 2010; Schmid et al., 2010) and one that involves the SC (Kato et al., 2011; Sahraie et al., 1997; Weiskrantz, 2009). The issue of blindsight therefore opens up debate on the involvement of the extrageniculate pathways in nonconscious perceptual and attention processes. Over the years, several experimental techniques have been successfully developed to assess nonconscious perception and its effects in healthy individuals. These techniques use "invisible" stimuli or render a stimulus completely invisible, and dedicated paradigms include, among others, binocular rivalry, subliminal stimuli, and visual masking. Yet, even though it has been shown that invisible stimuli can produce some changes in behavior (e.g., Kim & Blake, 2005; Roseboom & Arnold, 2011), whether such effects involve the extrageniculate pathways is not established. We review here only some of the main findings on this issue since readers can find extensive and comprehensive reviews elsewhere (Kim & Blake, 2005; Leopold, 2012; Lin & He, 2009; Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014; Tong, Meng, & Blake, 2006).

When different stimuli are presented to the two eyes, only one stimulus is seen at a time while the other is invisible because of

interocular suppression. Perception then alternates spontaneously between the two stimuli. This is called binocular rivalry. In one variant of this paradigm, continuously flashing shapes are presented to one eye while a less potent stimulus is presented to the other (Tsuchiya & Koch, 2005). The most salient stimulus dominates and the other stimulus is perceptually suppressed even though it is still physically present on the screen. In another variant, one stimulus is presented first monocularly, followed by binocular presentation of the two stimuli (Wilke, Logothetis, & Leopold, 2003). The stimulus presented first fades. In both cases, perceptual suppression is observed during prolonged periods.

During perceptual suppression, the activity of early and higher visual cortical areas is dramatically decreased (Fang & He, 2005; Yuval-Greenberg & Heeger, 2013), and such modulation was attributed to attention (Watanabe et al., 2011). Indeed, behavioral and electrophysiological studies have shown that attention plays a crucial role in dichoptic conflicts, and the effects of rivalry have been found to disappear without attention (Brascamp & Blake, 2012; Ling & Blake, 2012; Zhang, Jamison, Engel, He, & He, 2011). An interesting find was that perceptually suppressed stimuli still influence behavior (Blake, 2001). For instance, they can guide attention toward peripheral locations (Lin & He, 2009; Xu, Zhang, & Geng, 2011) and can trigger eye movement (Spering & Carrasco, 2015). A recent review by Spering and Carrasco (Spering & Carrasco, 2015) shed some light on the links between eye movements without awareness and perceptually suppressed stimuli. The authors proposed a network of structures involved in involuntary and controlled oculomotion and speculated that eye movements to invisible stimuli may depend on the extrageniculate pathways. Are the extrageniculate pathways really responsible for such effects? Unfortunately, extant data are insufficient to draw valid conclusions on the role of the extrageniculate pathways in the behavioral effects of perceptually suppressed stimuli (Sterzer et al., 2014). For instance, regarding physiological data, on one hand, deep electrophysiological recordings in monkeys showed that the firing rate of neurons in the pulvinar was affected by perceptual suppression, but not of those in the LGN, suggesting that the geniculate pathway is driven exclusively by the physical presence of a stimulus (Haynes, Tregellas, & Rees, 2005; Tong et al., 2006; Wilke, Mueller, & Leopold, 2009; Wunderlich, Schneider, & Kastner, 2005). On the other hand, during perceptual suppression, some pulvinar cells show excitatory and others inhibitory spiking modulation, typically related to the on and offset responses to a physical target. This suggests that activity in the pulvinar is closely related to the perception of a stimulus (Wilke et al., 2009), be it with or without awareness, precluding the hypothesis that it would be specifically involved in the processing of invisible stimuli. This is hardly surprising if we consider that rivalry involves a stage at which input from the two eyes is integrated in a way that the most salient one dominates (Brascamp, Klink, & Levelt, 2015; Carmel, Arcaro, Kastner, & Hasson, 2010). Such integration necessarily involves higher cortical structures (Tong et al., 2006) and this would further preclude interocular suppression from being a candidate for testing extrageniculate effects.

Unlike binocular rivalry wherein it is interocular suppression that determines awareness of a stimulus, awareness in masking paradigms is determined by manipulating the physical properties of visual stimulation. Applied to the study of attention, some of these methods consist in presenting, in a peripheral cueing para-

digm, spatial cues that are invisible to the participant and that are followed by a well visible target to detect. The brief presentation of low contrast cues that are below perceptual threshold, of tiny spatial cues only a few pixels large, or of cues that are in close temporal proximity to the target guide spatial attention and, in some cases, eye movements, without awareness (Spering & Carrasco, 2015). They even produce unconscious distracting effects if they are not task-relevant (Ansorge, 2003; Lambert, Naikar, McLachlan, & Aitken, 1999; McCormick, 1997; Mele, Savazzi, Marzi, & Berlucchi, 2008; Mulckhuysse & Theeuwes, 2010a; Van der Stigchel, Mulckhuysse, & Theeuwes, 2009). However, once again, the question is whether the effects of such invisible cues on attention and saccadic eye movements involve the extrageniculate pathways. In a review of such effects, Mulckhuysse and Theeuwes (2010a) suggested that unconscious overt and covert attentional orienting depends on the fast extrageniculate pathways, particularly the retino-tectal one. The authors argued on the basis of the similarities between the attention effects and those of invisible emotional information. Furthermore, they argued that since changes in oculomotor behavior originate in the SC, then oculomotor effects triggered by unperceived stimuli would also involve collicular processing (Huxlin et al., 2009; Rothkirch, Stein, Sekutowicz, & Sterzer, 2012; Spering, Pomplun, & Carrasco, 2011; Tamietto et al., 2010). Even though this makes sense and some empirical data show nasal-temporal asymmetries in orienting to invisible stimuli (Mulckhuysse & Theeuwes, 2010b), to our knowledge, no direct and clear-cut demonstration of the extrageniculate mediation of such unconscious attentional effects was ever made. A study by Bauer and colleagues (Bauer, Cheadle, Parton, Müller, & Usher, 2009) used below awareness flickering Gabor patches that facilitated subsequent target detection. The authors interpreted these attentional effects as the modulation of neural γ band activity, associated with top-down attentional modulation (Vidal, Chaudmon, O'Regan, & Tallon-Baudry, 2006). While arguing in favor of an attention- γ hypothesis that would rely on the geniculate pathway, the authors omitted to recall that a disynaptic pathway conveys motion signals from the retina to the cortex through the pulvinar (Benevento & Miller, 1981; Petersen, Robinson, & Keys, 1985; Villeneuve, Kupers, Gjedde, Ptito, & Casanova, 2005) and the SC (Boehnke & Munoz, 2008; Dean, Redgrave, & Westby, 1989; Lyon et al., 2010; Sahibzada, Dean, & Redgrave, 1986) that are extremely responsive to such signals. Thus, the authors left out the explanation that the unconsciously perceived flickering stimuli could have triggered extrageniculate responses to perceived motion, rather than mimicking in the LGN the attentional tagging of the cortico-geniculate γ feedback.

Another method for rendering stimuli invisible and suppressing their perception is masking. In a typical variant of the masking paradigm, a first stimulus is briefly presented and substituted shortly after by another stimulus, the mask (i.e., backward masking). The mask suppresses the former from perception (Breitmeyer, 1984; Breitmeyer & Ogmen, 2000). Several studies have shown that masked peripheral visual spatial cues can still attract attention to their location and modulate processing of subsequent targets (Palmer & Mattler, 2013a, 2013b; Reuss, Kiesel, Kunde, & Wühr, 2012). It seems that masking reduces neural responses to the masked stimulus at early and middle stages of visual processing (Green et al., 2005), suggesting that their effects on behavior reach later stages of visual processing through routes other than the

one involving the LGN and the primary visual cortex that is thought to be the locus where masking exerts its influence (Macknik & Livingstone, 1998; Schiller, 1968). On the other hand, using masking methods, it was demonstrated that facial expressions and other emotional stimuli attract attention to their location in an involuntary fashion (e.g., Pourtois, Grandjean, Sander, & Vuilleumier, 2004). An interesting find was that several other findings suggest that the extrageniculate pathways are involved in the unconscious processing of emotional stimuli (Liddell et al., 2005; Morris, Öhman, & Dolan, 1999; Troiani & Schultz, 2013). For instance, it was reported that masked fearful faces that are not perceived consciously activate emotion-related structures such as the amygdala, but they also activate the SC and the pulvinar. It was, therefore, postulated (Liddell et al., 2005) that an automatic and unconscious alarm colliculo-pulvino-amygdalar network acts for rapid processing of threatening information. Such a network was recently identified in humans through imaging techniques (Tamietto, Pullens, de Gelder, Weiskrantz, & Goebel, 2012). However, does orienting attention toward the location of such unconscious stimuli involve the extrageniculate pathways? In fact, even though there are some hypotheses that this might be the case (Vuilleumier & Schwartz, 2001), the literature is not clear on that issue either since the exact role of the SC and the pulvinar during processing of masked emotional stimuli has not been clearly differentiated empirically from the role of the amygdala.

In summary, these findings suggest that stimuli that are perceptually suppressed do guide attention (Lin & He, 2009; Mulckhuysse & Theeuwes, 2010a), and the similarity with the unconscious effects found for stimuli presented in the blind field of patients with blindsight is noticeable (Leopold, 2012; Spering & Carrasco, 2015). However, the extant literature provides quite a puzzling picture about the fate of perceptually suppressed stimuli at a neural level. Some data suggest that perceptual suppression already acts on the earliest stages of visual processing, that is, the LGN and the primary visual cortex. These implicitly suggest that pathways that bypass the LGN and the occipital cortex must be responsible for the effects of perceptually suppressed stimuli. These are the extrageniculate pathways.

However, the involvement of extrageniculate structures in the guidance of behavior and attention by perceptually suppressed stimuli is particularly scarce and was reported only within specific contexts (Leopold, 2012; Sterzer et al., 2014; Troiani & Schultz, 2013). Harsh conclusions should be therefore avoided.

Discussion

Main Limits

As stated earlier, the main limitation of using behavioral cues is that the results do not directly attest to the involvement and role of the neural pathways of interest. Instead, the techniques reviewed here were developed based on the knowledge of some anatomical and physiological particularities of the visual system and more specifically, of the extrageniculate pathways. Therefore, even though the results cannot be interpreted as directly reflecting the function of these pathways, they are to be understood as aids for gathering clues about their contribution. Nevertheless, this kind of caveat is also present but the other way around when using imaging techniques that are supposed to assess more directly the

involvement of the brain structures in cognitive processes. In fact, accounting for the activation of the nervous system as the direct representation of the specific cognitive processes involved in a specific task is merely a postulate (Bunge & Kahn, 2009).

Yet, many questions are still to be answered. The first concerns spatial orienting as mentioned earlier. Nasal-temporal asymmetries in oculomotor behavior are somewhat puzzling since different effects are found for different parameters of eye movement (Lewis et al., 1985). An explanation of such discrepancies was proposed by Jóhannesson and colleagues (Jóhannesson et al., 2012) in terms of speed/accuracy tradeoffs. Indeed, they found significantly higher accuracy in somewhat slower but not significant latencies (1 to 10 ms slower) in the temporal field than in the nasal field, evoking a speed/accuracy tradeoff. Unfortunately, such an interpretation cannot hold as reliable and significant speed/accuracy tradeoffs have not been evidenced. The absence of reliable results may come from the small samples tested (5 to 14 participants). Finally, even if such tradeoffs were demonstrated, it would be difficult to interpret the results in terms of neural and cognitive underlying processes. Alternatively, Bompas and Sumner proposed a theoretical dissociation between saccadic choice and latency (Bompas & Sumner, 2011). The choice of the stimulus to attend to would be subtended by specific cognitive systems and dedicated pathways, probably explaining why asymmetries would be found with one parameter but not with another. In studies having investigated behavioral nasal-temporal asymmetries, distinct results were found in reaction time (RT) and accuracy, which backup the dissociation hypothesis (Michael & Gálvez-García, 2011; Mizzi & Michael, 2014). This aspect per se is still controversial and appeals to extensive researches, because investigations exploit differences between behavioral cues as indicative of different phenomena instead of different aspects of a common process (Ratcliff & Rouder, 1998), or in terms of speed/accuracy tradeoffs (Jóhannesson et al., 2012). Therefore, future researchers should try to understand what exactly produces different patterns in nasal-temporal asymmetries as a function of the dependent variable, be it oculomotor or behavioral. It seems that an investigation—or a methodological review—of a wide range of parameters is needed. With the aim of conciliating the different variables, one can attempt to replicate the results of the conflicting studies (Bompas & Sumner, 2011; Jóhannesson et al., 2012; Mizzi & Michael, 2014) in a homogeneous investigation of those effects.

Another aspect of extrageniculate mediation that needs extensive investigation is its role in nonspatial selection and resolution. Both the SC and the pulvinar are thought to be involved in attentional selection (Buchsbaum et al., 2006; Fischer & Whitney, 2012; Knudsen, 2011; Lovejoy & Krauzlis, 2010; Rotshtein et al., 2011; Strumpf et al., 2013), but the way they process information is seemingly different (LaBerge, 1990). One of these differences presumably resides in resolution. For instance, LaBerge (1990) suggested that collicular computations suffice to orient attention toward a target as long as it is not presented on a clustered background. If this were the case, then visual resolution and selection of targets among distractors would require the pulvinar. This leads to the hypothesis that potential nasal-temporal asymmetries in tasks requiring a certain level of resolution for targets to be correctly processed could be informative as to which of the SC or the pulvinar is mostly involved. This could be done through varying target-distractor spatial proximity and physical similarity.

In fact if a temporal superiority is found only for displays requiring low resolution, then a collicular origin could be suspected. If by contrast, such temporal superiority is found only for displays requiring high resolution, then a pulvinar origin could be suspected. And of course, if temporal superiorities are found in all kinds of display, then a whole extrageniculate involvement could be postulated. Unfortunately, Michael and Ojeda (2005) did not find any nasal-temporal asymmetries in a task where the target distractor similarity varied parametrically. A more recent investigation did, however, provide some data on this issue (Michael et al., 2016). This, however, should not discourage further researches in as much as negative result are not of substantial value, and in as much as the effects of spatial proximity have not been investigated yet. A complementary line of investigation should concern the combination of monocular viewing conditions with the S-cones stimuli isolation technique. This would give even more insight into the role of extrageniculate structures in visual resolution and selection. In fact, no exploration of nasal-temporal asymmetries with the S-cone isolation technic in tasks of visual resolution and selection has yet been reported. One can expect S-cone stimulation not to exert such asymmetry if the physiological origin of this phenomenon is indeed retino-tectal. This kind of results can bring new arguments in favor of both nasal-temporal asymmetries and S-cone isolation technics as relevant cues of the extrageniculate modulation in attention. Moreover, with the use of both manual and saccadic measures, such a study can also provide crucial new data regarding the inconsistent literature on the influence of S-cone stimulation above-mentioned.

Then again, the S-cone method is also subject to ongoing debates. On one hand, the overall technique is problematic. As discussed earlier, it seems to vary along studies and aspects such as the color calibration of stimuli (Boynton & Kaiser, 1978; Smithson et al., 2003; Webster & Mollon, 1994) or the presentation parameters of the stimuli (e.g., luminance or size, see Mizzi & Michael, 2014; Sumner et al., 2004) have never benefitted from a comprehensive and comparative methodological review. This inconsistency appears challenging when it comes to interpret and to link cognitive processes (e.g., attentional capture and progression; Mizzi & Michael, 2014) to dependent variables (e.g., oculomotor distractor effect and saccadic IOR; Sumner et al., 2002, 2004). On the other hand, the most controversial aspect of the literature is whether or not the S-cone stimulation bypasses the SC. Despite the lack of evidence on direct retino-tectal transfer of color information, the recent work of Hall and Colby (Hall & Colby, 2014) measured collicular responses to S-cone stimuli, and the hypothesis of corticofugal projections to the SC has been formulated (Hall & Colby, 2014; Mizzi & Michael, 2014). This aspect is crucial since Hall and Colby's results challenge the conclusions of numerous researches conducted on the basis of this technique, urging for further investigations. The temporal aspects of the transfer of visual information can be used to assess the direct activation versus retro-activation of the SC after S-cone presentation. One can directly test this hypothesis by comparing latencies of collicular neurons' response to contrast versus S-cone stimuli through intracranial EEG measurements in monkeys (Hall & Colby, 2014; Jayakumar, Dreher, & Vidyasagar, 2013). Another approach would be to use the temporal asynchrony hypothesis in transfer time between the geniculate and extrageniculate pathways (Chambers et al., 2004; Mulckhuyse & Theeuwes, 2010a). Fol-

lowing the most accepted view of sequential activation, the geniculate pathway is thought to convey information more slowly than the extrageniculate ones. Combining EEG techniques with psychophysical techniques of S-cone stimuli isolation in human could result in particular patterns of brain activity. In fact, it could be expected that contrast stimuli that are processed through both pathways could trigger a prime parietal activation followed by an occipital one, signaling the abovementioned asynchrony. As for S-cone stimuli, a prime occipital activation could be expected, signaling a decreased transfer of information from the extrageniculate pathways to the parietal cortices.

As mentioned earlier, the neural bases of perceptual suppression are still poorly understood, as is the potential role of the extrageniculate pathways in the perception of perceptually suppressed stimuli. It would be quite informative if nasal-temporal asymmetries were found in perceptual suppression. For instance, because each eye is stimulated separately in a binocular rivalry setting (Tsuchiya & Koch, 2005), it is possible to assess the effects of nasal and temporal stimulations for each eye. If extrageniculate pathways are involved in perceptual suppression, one could expect asymmetries whether or not the stimulus is perceptually suppressed. It was shown that stimuli that are not consciously perceived can trigger attentional reorienting (Xu et al., 2011). Is there a temporal field superiority for such an effect? Such observation could constitute a reliable cue in favor of the involvement of the extrageniculate pathways in perceptual suppression.

Promising Trends and Open Questions

The use of the psychophysical techniques presented here that investigate behavioral cues of the involvement of the extrageniculate pathways have helped to refine cognitive models of attention. Regarding automatic attention, the early Koch and Ullman model (Koch & Ullman, 1985) proposed that attention would be oriented in space in a winner-take-all fashion, based on the proximity and similarity of the items presented in the visual field. The focus of attention would progress from the most salient element to the least salient one, inhibiting each already explored location to progress. This is very close to the way Posner and Petersen considered the behavior of the focus of attention, going from attentional engagement to disengagement, inhibition and then moving away (Posner & Petersen, 1990). This conception of a unique serial process has been modified since capture and progression of attention had been shown to be different when the retino-tectal pathway is solicited. For instance, capture of attention is possible with S-cone stimulation, while attentional progression on the basis of salience is not (Mizzi & Michael, 2014; Sumner et al., 2002), suggesting that these components are independent. The same logic applies to the dissociation between attentional and oculomotor automatic processes that have been long thought to rely on the same neural structures and to share cognitive processes (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Kustov & Robinson, 1996; Moore, Armstrong, & Fallah, 2003; Rizzolatti et al., 1987; Shipp, 2004). It has been shown that the use of S-cone stimuli impacts oculomotor distraction, but not attentional distraction (Bompas & Sumner, 2009; Sumner et al., 2004), also suggesting independent processes. Therefore, theoretical conceptions of attention are modified and refined thanks to the use of such techniques and the information they allow us to collect.

The behavioral cues of the involvement of the extrageniculate pathways can also give new arguments from psychological sciences to refine neurophysiological models. For instance, the neuroimaging-based model of Corbetta and Shulman (Corbetta & Shulman, 2002) proposed a double interacting cortical network that subtends controlled and automatic attention, the latter being strongly lateralized in the right hemisphere. The authors only acknowledged the importance of ascending subcortical pathways by hypothesizing that the right hemisphere lateralization of automatic processes could be because of the denser concentration of noradrenaline in the right part of the thalamus, compared with the left part (Oke, Keller, Mefford, & Adams, 1978). Besides this aspect, the authors do not argue about the origin of the subcortical activation. The contribution of psychological sciences could be to propose that the extrageniculate pathways are playing such a role. Indeed, the argument of Corbetta and Shulman is based on the observation that noradrenergic systems are involved in selective attention to salient stimuli (Aston-Jones, Foote, & Bloom, 1984; Pardo, Fox, & Raichle, 1991). Studies relying on nasal-temporal asymmetries (Michael & Gálvez-García, 2011) and S-cone isolation techniques (Mizzi & Michael, 2014) suggest that attention to salient stimuli mostly relies on extrageniculate processing in the right hemisphere. Once again, the results of such behavioral studies shed light on some aspects of theoretical models by describing further the role of the extrageniculate pathways. It seems then evident to state that the link between neurological and behavioral aspects is of the utmost importance and has to be central in future investigations. Even though imaging techniques are more accessible nowadays, behavioral studies relying on psychophysical techniques, such as the ones described in this review, are not to be undervalued because they provide stable and easily replicable results, along with reliable cues regarding the neural processes involved.

A central question that remains open is the influence of descending cortical projections on extrageniculate structures in attentional processing, be it covert or overt. Discrepancies in the literature on nasal-temporal asymmetries have led some authors to question their extrageniculate mediation (Honda, 2002; Jóhannesson et al., 2012). Rather, cortical control has been highlighted. For instance, involuntary eye movements are thought to be inhibited by fronto-tectal projections (Fries, 1984; Sommer & Wurtz, 2000; Wilson & Toyne, 1970), while parieto-tectal projections seem to mediate visuomotor transformations that process information into representation that can be used to guide action (Burman & Bruce, 1997; Ferraina, Paré, & Wurtz, 2002; Machado & Rafal, 2004a; Müri et al., 1998; Ploner et al., 2005). This suggests that cortico-subcortical projections are involved in attention and eye movements, leading us to wonder what would be their role in the rise of nasal-temporal asymmetries. Thus, it is still necessary to build a comprehensive model that combines neural and psychological processes, since numerous patient (Machado & Rafal, 2004a, 2004b; Ploner et al., 2005; Rafal, 2006), neurological (Burman & Bruce, 1997; Müri et al., 1998), physiological (Ferraina et al., 2002), and animal (Gaymard et al., 2003) data can find only tentative completion in neural models of oculomotion (Corbetta & Shulman, 2002; Rafal, 2006; Spering & Carrasco, 2015).

Investigations of preparatory attention might constitute a future direction. As stated in the triangular circuit theory (LaBerge, 2002), attention involves the modulation of pulvinar activity by

frontal areas. When the observer knows where or what to expect in a visual search task before the display appears, frontal modulation allows the pulvinar to increase activity in posterior cortical areas for subsequent processing to be optimal. Can nasal-temporal asymmetries be more pronounced when expecting specific stimuli to occur, or when expecting stimuli to occur at specific locations? Furthermore, the investigation of nasal-temporal asymmetries in such settings could combine with psychophysical techniques using S-cones stimuli that are invisible to the retino-tectal pathway could offer clues about the way the extrageniculate pathways are involved in preparatory attention.

Conclusions

Overall, the role of the extrageniculate pathways as a fundamental set of structures in visual attention becomes clearer as the precision of techniques used in neurophysiological, neuropsychological, and neuroimaging investigations increases. Experimental psychologists have contributed and still contribute considerably to this through the use of three behavioral cues, considered to reflect the functions of the extrageniculate pathways: nasal-temporal asymmetries, responses to S-cone stimuli, and to perceptually suppressed stimuli. Each of these three cues is problematic in that there is some (even though unequivocal) evidence running counter to the idea that they reflect extrageniculate mediation. However, findings are far more convergent when it comes to point out that nasal-temporal asymmetries and performance for S-cones stimuli are plausible cues of extrageniculate mediation of attention effects, in contrast to performance for perceptually suppressed stimuli. Future research should target the points of debate mentioned earlier to better establish the way the extrageniculate pathways contribute to the rise of each of the three behavioral cues.

References

- Adams, M. M., Hof, P. R., Gattass, R., Webster, M. J., & Ungerleider, L. G. (2000). Visual cortical projections and chemoarchitecture of macaque monkey pulvinar. *The Journal of Comparative Neurology*, 419, 377–393. [http://dx.doi.org/10.1002/\(SICI\)1096-9861\(20000410\)419:3<377::AID-CNE9>3.0.CO;2-E](http://dx.doi.org/10.1002/(SICI)1096-9861(20000410)419:3<377::AID-CNE9>3.0.CO;2-E)
- Ansorge, U. (2003). Asymmetric influences of temporally vs. nasally presented masked visual information: Evidence for collicular contributions to nonconscious priming effects. *Brain and Cognition*, 51, 317–325. [http://dx.doi.org/10.1016/S0278-2626\(03\)00034-4](http://dx.doi.org/10.1016/S0278-2626(03)00034-4)
- Anstis, S. M., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. *Colour Vision: Physiology and Psychophysics*, 155–166.
- Arend, I., Machado, L., Ward, R., McGrath, M., Ro, T., & Rafal, R. D. (2008). The role of the human pulvinar in visual attention and action: Evidence from temporal-order judgment, saccade decision, and antisaccade tasks. *Progress in Brain Research*, 171, 475–483. [http://dx.doi.org/10.1016/S0079-6123\(08\)00669-9](http://dx.doi.org/10.1016/S0079-6123(08)00669-9)
- Aston-Jones, G., Foote, S. L., & Bloom, F. E. (1984). *Frontiers of clinical neuroscience* (Ziegler, M. G.). Baltimore, MD: Williams & Wilkins.
- Baizer, J. S., Desimone, R., & Ungerleider, L. G. (1993). Comparison of subcortical connections of inferior temporal and posterior parietal cortex in monkeys. *Visual Neuroscience*, 10, 59–72. <http://dx.doi.org/10.1017/S0952523800003229>
- Bauer, F., Cheadle, S. W., Parton, A., Müller, H. J., & Usher, M. (2009). Gamma flicker triggers attentional selection without awareness. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 1666–1671. <http://dx.doi.org/10.1073/pnas.0810496106>
- Benevento, L. A., & Miller, J. (1981). Visual responses of single neurons in the caudal lateral pulvinar of the macaque monkey. *The Journal of Neuroscience*, 1, 1268–1278.
- Berger, A., & Henik, A. (2000). The endogenous modulation of IOR is nasal-temporal asymmetric. *Journal of Cognitive Neuroscience*, 12, 421–428. <http://dx.doi.org/10.1162/089892900562246>
- Berman, R. A., & Wurtz, R. H. (2008). Exploring the pulvinar path to visual cortex. *Progress in Brain Research*, 171, 467–473. [http://dx.doi.org/10.1016/S0079-6123\(08\)00668-7](http://dx.doi.org/10.1016/S0079-6123(08)00668-7)
- Berman, R. A., & Wurtz, R. H. (2010). Functional identification of a pulvinar path from superior colliculus to cortical area MT. *The Journal of Neuroscience*, 30, 6342–6354. <http://dx.doi.org/10.1523/JNEUROSCI.6176-09.2010>
- Berman, R. A., & Wurtz, R. H. (2011). Signals conveyed in the pulvinar pathway from superior colliculus to cortical area MT. *The Journal of Neuroscience*, 31, 373–384. <http://dx.doi.org/10.1523/JNEUROSCI.4738-10.2011>
- Bisley, J. W. (2011). The neural basis of visual attention. *The Journal of Physiology*, 589, 49–57. <http://dx.doi.org/10.1113/jphysiol.2010.192666>
- Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain and Mind*, 2, 5–38. <http://dx.doi.org/10.1023/A:1017925416289>
- Boehne, S. E., & Munoz, D. P. (2008). On the importance of the transient visual response in the superior colliculus. *Current Opinion in Neurobiology*, 18, 544–551. <http://dx.doi.org/10.1016/j.conb.2008.11.004>
- Bompas, A., Sterling, T., Rafal, R. D., & Sumner, P. (2008). Naso-temporal asymmetry for signals invisible to the retinotectal pathway. *Journal of Neurophysiology*, 100, 412–421. <http://dx.doi.org/10.1152/jn.90312.2008>
- Bompas, A., & Sumner, P. (2009). Oculomotor distraction by signals invisible to the retinotectal and magnocellular pathways. *Journal of Neurophysiology*, 102, 2387–2395. <http://dx.doi.org/10.1152/jn.00359.2009>
- Bompas, A., & Sumner, P. (2011). *Are choice and latency dissociable?* Presented at the European Conference on Eye Movements, Vienna, Austria.
- Boynton, R. M., & Kaiser, P. K. (1978). Temporal analog of the minimally distinct border. *Vision Research*, 18, 111–113. [http://dx.doi.org/10.1016/0042-6989\(78\)90085-8](http://dx.doi.org/10.1016/0042-6989(78)90085-8)
- Brascamp, J. W., & Blake, R. (2012). Inattention abolishes binocular rivalry: Perceptual evidence. *Psychological Science*, 23, 1159–1167. <http://dx.doi.org/10.1177/0956797612440100>
- Brascamp, J. W., Klink, P. C., & Levelt, W. J. M. (2015). The “laws” of binocular rivalry: 50 years of Levelt’s propositions. *Vision Research*, 109 (Part A), 20–37. <http://doi.org/10.1016/j.visres.2015.02.019>
- Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. New York, NY: Oxford University Press.
- Breitmeyer, B. G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review, and update. *Perception & Psychophysics*, 62, 1572–1595. <http://dx.doi.org/10.3758/BF03212157>
- Buchsbaum, M. S., Buchsbaum, B. R., Chokron, S., Tang, C., Wei, T.-C., & Byne, W. (2006). Thalamocortical circuits: FMRI assessment of the pulvinar and medial dorsal nucleus in normal volunteers. *Neuroscience Letters*, 404, 282–287. <http://dx.doi.org/10.1016/j.neulet.2006.05.063>
- Bunge, S. A., & Kahn, I. (2009). Cognition: An overview of neuroimaging techniques. In L. R. Squire (Ed.), *Encyclopedia of neuroscience* (pp. 1063–1067). Oxford, UK: Academic Press. Retrieved from <http://www.sciencedirect.com/science/article/pii/B9780080450469002989>; <http://dx.doi.org/10.1016/B978-008045046-9.00298-9>
- Burman, D. D., & Bruce, C. J. (1997). Suppression of task-related saccades by electrical stimulation in the primate’s frontal eye field. *Journal of Neurophysiology*, 77, 2252–2267.

- Calkins, D. J. (2001). Seeing with S cones. *Progress in Retinal and Eye Research*, 20, 255–287. [http://dx.doi.org/10.1016/S1350-9462\(00\)00026-4](http://dx.doi.org/10.1016/S1350-9462(00)00026-4)
- Carmel, D., Arcaro, M., Kastner, S., & Hasson, U. (2010). How to create and use binocular rivalry. *Journal of Visualized Experiments*, 45, e2030. <http://dx.doi.org/10.3791/2030>
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, 51, 1484–1525. <http://dx.doi.org/10.1016/j.visres.2011.04.012>
- Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience*, 7, 217–218. <http://dx.doi.org/10.1038/nn1203>
- Clower, D. M., West, R. A., Lynch, J. C., & Strick, P. L. (2001). The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. *The Journal of Neuroscience*, 21, 6283–6291.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3, 201–215. <http://dx.doi.org/10.1038/nrn755>
- Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Review of Neuroscience*, 34, 569–599. <http://dx.doi.org/10.1146/annurev-neuro-061010-113731>
- Cotton, P. L., & Smith, A. T. (2007). Contralateral visual hemifield representations in the human pulvinar nucleus. *Journal of Neurophysiology*, 98, 1600–1609. <http://dx.doi.org/10.1152/jn.00419.2007>
- Cowey, A. (2010). Visual system: How does blindsight arise? *Current Biology*, 20, R702–R704. <http://dx.doi.org/10.1016/j.cub.2010.07.014>
- Cowey, A., & Stoerig, P. (1991). The neurobiology of blindsight. *Trends in Neurosciences*, 14, 140–145. [http://dx.doi.org/10.1016/0166-2236\(91\)90085-9](http://dx.doi.org/10.1016/0166-2236(91)90085-9)
- Curcio, C. A., & Allen, K. A. (1990). Topography of ganglion cells in human retina. *The Journal of Comparative Neurology*, 300, 5–25. <http://dx.doi.org/10.1002/cne.903000103>
- Dean, P., Redgrave, P., & Westby, G. W. (1989). Event or emergency? Two response systems in the mammalian superior colliculus. *Trends in Neurosciences*, 12, 137–147. [http://dx.doi.org/10.1016/0166-2236\(89\)90052-0](http://dx.doi.org/10.1016/0166-2236(89)90052-0)
- de Monasterio, F. M. (1978). Properties of ganglion cells with atypical receptive-field organization in retina of macaques. *Journal of Neurophysiology*, 41, 1435–1449.
- Denny-Brown, D., & Chambers, C. D. (1955). Visuomotor functions in the cerebral cortex. *Journal of Nervous and Mental Disease*, 121, 288–289.
- Everling, S., & Fischer, B. (1998). The antisaccade: A review of basic research and clinical studies. *Neuropsychologia*, 36, 885–899. [http://dx.doi.org/10.1016/S0028-3932\(98\)00020-7](http://dx.doi.org/10.1016/S0028-3932(98)00020-7)
- Fahle, M., & Schmid, M. (1988). Naso-temporal asymmetry of visual perception and of the visual cortex. *Vision Research*, 28, 293–300. [http://dx.doi.org/10.1016/0042-6989\(88\)90157-5](http://dx.doi.org/10.1016/0042-6989(88)90157-5)
- Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, 8, 1380–1385. <http://dx.doi.org/10.1038/nn1537>
- Fecteau, J. H., & Munoz, D. P. (2006). Saliency, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences*, 10, 382–390. <http://dx.doi.org/10.1016/j.tics.2006.06.011>
- Ferraina, S., Paré, M., & Wurtz, R. H. (2002). Comparison of cortico-cortical and cortico-collicular signals for the generation of saccadic eye movements. *Journal of Neurophysiology*, 87, 845–858.
- Fischer, J., & Whitney, D. (2012). Attention gates visual coding in the human pulvinar. *Nature Communications*, 3, 1051. <http://dx.doi.org/10.1038/ncomms2054>
- Fries, W. (1984). Cortical projections to the superior colliculus in the macaque monkey: A retrograde study using horseradish peroxidase. *The Journal of Comparative Neurology*, 230, 55–76. <http://dx.doi.org/10.1002/cne.902300106>
- Gaymard, B., Lynch, J., Ploner, C. J., Condy, C., & Rivaud-Péchoix, S. (2003). The parieto-collicular pathway: Anatomical location and contribution to saccade generation. *European Journal of Neuroscience*, 17, 1518–1526. <http://dx.doi.org/10.1046/j.1460-9568.2003.02570.x>
- Goldberg, M. E., & Wurtz, R. H. (1972). Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *Journal of Neurophysiology*, 35, 560–574.
- Green, M. F., Glahn, D., Engel, S. A., Nuechterlein, K. H., Sabb, F., Strojwas, M., & Cohen, M. S. (2005). Regional brain activity associated with visual backward masking. *Journal of Cognitive Neuroscience*, 17, 13–23. <http://dx.doi.org/10.1162/0898929052880011>
- Habekost, T., & Rostrup, E. (2006). Persisting asymmetries of vision after right side lesions. *Neuropsychologia*, 44, 876–895. <http://dx.doi.org/10.1016/j.neuropsychologia.2005.09.002>
- Hall, N., & Colby, C. (2014). S-cone visual stimuli activate superior colliculus neurons in old world monkeys: Implications for understanding blindsight. *Journal of Cognitive Neuroscience*, 26, 1234–1256. http://dx.doi.org/10.1162/jocn_a_00555
- Harting, J. K., Huerta, M. F., Frankfurter, A. J., Strominger, N. L., & Royce, G. J. (1980). Ascending pathways from the monkey superior colliculus: An autoradiographic analysis. *The Journal of Comparative Neurology*, 192, 853–882. <http://dx.doi.org/10.1002/cne.901920414>
- Haynes, J.-D., Tregellas, J., & Rees, G. (2005). Attentional integration between anatomically distinct stimulus representations in early visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 14925–14930. <http://dx.doi.org/10.1073/pnas.0501684102>
- Hendrickson, A., Wilson, M. E., & Toyne, M. J. (1970). The distribution of optic nerve fibers in *Macaca mulatta*. *Brain Research*, 23, 425–427. [http://dx.doi.org/10.1016/0006-8993\(70\)90068-5](http://dx.doi.org/10.1016/0006-8993(70)90068-5)
- Hendry, S. H. C., & Reid, R. C. (2000). The koniocellular pathway in primate vision. *Annual Review of Neuroscience*, 23, 127–153. <http://dx.doi.org/10.1146/annurev.neuro.23.1.127>
- Himmelbach, M., Erb, M., & Karnath, H.-O. (2007). Activation of superior colliculi in humans during visual exploration. *BMC Neuroscience*, 8, 66. <http://dx.doi.org/10.1186/1471-2202-8-66>
- Honda, H. (2002). Idiosyncratic left-right asymmetries of saccadic latencies: Examination in a gap paradigm. *Vision Research*, 42, 1437–1445. [http://dx.doi.org/10.1016/S0042-6989\(02\)00050-0](http://dx.doi.org/10.1016/S0042-6989(02)00050-0)
- Hubel, D. H., LeVay, S., & Wiesel, T. N. (1975). Mode of termination of retinotectal fibers in macaque monkey: An autoradiographic study. *Brain Research*, 96, 25–40. [http://dx.doi.org/10.1016/0006-8993\(75\)90567-3](http://dx.doi.org/10.1016/0006-8993(75)90567-3)
- Huxlin, K. R., Martin, T., Kelly, K., Riley, M., Friedman, D. I., Burgin, W. S., & Hayhoe, M. (2009). Perceptual relearning of complex visual motion after V1 damage in humans. *The Journal of Neuroscience*, 29, 3981–3991. <http://dx.doi.org/10.1523/JNEUROSCI.4882-08.2009>
- Ignashchenkova, A., Dicke, P. W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nature Neuroscience*, 7, 56–64. <http://dx.doi.org/10.1038/nn1169>
- Itaya, S. K., & Van Hoesen, G. W. (1983). Retinal projections to the inferior and medial pulvinar nuclei in the Old-World monkey. *Brain Research*, 269, 223–230. [http://dx.doi.org/10.1016/0006-8993\(83\)90131-2](http://dx.doi.org/10.1016/0006-8993(83)90131-2)
- Jayakumar, J., Dreher, B., & Vidyasagar, T. R. (2013). Tracking blue cone signals in the primate brain. *Clinical & Experimental Optometry*, 96, 259–266. <http://dx.doi.org/10.1111/j.1444-0938.2012.00819.x>
- Jóhannesson, Ó. I., Asgeirsson, A. G., & Kristjánsson, A. (2012). Saccade performance in the nasal and temporal hemifields. *Experimental Brain Research*, 219, 107–120. <http://dx.doi.org/10.1007/s00221-012-3071-2>
- Jóhannesson, Ó. I., & Kristjánsson, A. (2013). Violating the main sequence: Asymmetries in saccadic peak velocities for saccades into the

- temporal versus nasal hemifields. *Experimental Brain Research*, 227, 101–110. <http://dx.doi.org/10.1007/s00221-013-3490-8>
- Johnson, M. H. (1990). Cortical maturation and the development of visual attention in early infancy. *Journal of Cognitive Neuroscience*, 2, 81–95. <http://dx.doi.org/10.1162/jocn.1990.2.2.81>
- Karnath, H.-O., Himmelbach, M., & Rorden, C. (2002). The subcortical anatomy of human spatial neglect: Putamen, caudate nucleus and pulvinar. *Brain: A Journal of Neurology*, 125, 350–360. <http://dx.doi.org/10.1093/brain/awf032>
- Kato, R., Takaura, K., Ikeda, T., Yoshida, M., & Isa, T. (2011). Contribution of the retino-tectal pathway to visually guided saccades after lesion of the primary visual cortex in monkeys. *European Journal of Neuroscience*, 33, 1952–1960. <http://dx.doi.org/10.1111/j.1460-9568.2011.07729.x>
- Kentridge, R. W. (2012). Blindsight: Spontaneous scanning of complex scenes. *Current Biology*, 22, R605–R606. <http://dx.doi.org/10.1016/j.cub.2012.06.011>
- Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings Biological Sciences*, 266, 1805–1811. <http://dx.doi.org/10.1098/rspb.1999.0850>
- Kim, C.-Y., & Blake, R. (2005). Psychophysical magic: Rendering the visible ‘invisible’. *Trends in Cognitive Sciences*, 9, 381–388. <http://dx.doi.org/10.1016/j.tics.2005.06.012>
- Kingstone, A., Friesen, C. K., & Gazzaniga, M. S. (2000). Reflexive joint attention depends on lateralized cortical connections. *Psychological Science*, 11, 159–166. <http://dx.doi.org/10.1111/1467-9280.00232>
- Knudsen, E. I. (2011). Control from below: The role of a midbrain network in spatial attention. *European Journal of Neuroscience*, 33, 1961–1972. <http://dx.doi.org/10.1111/j.1460-9568.2011.07696.x>
- Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: Towards the underlying neural circuitry. *Human Neurobiology*, 4, 219–227.
- Krauzlis, R. J., Liston, D., & Carello, C. D. (2004). Target selection and the superior colliculus: Goals, choices and hypotheses. *Vision Research*, 44, 1445–1451. <http://dx.doi.org/10.1016/j.visres.2004.01.005>
- Krauzlis, R. J., Lovejoy, L. P., & Zénon, A. (2013). Superior colliculus and visual spatial attention. *Annual Review of Neuroscience*, 36, 165–182. <http://dx.doi.org/10.1146/annurev-neuro-062012-170249>
- Kristjánsson, A., Vandenbroucke, M. W. G., & Driver, J. (2004). When pros become cons for anti- versus prosaccades: Factors with opposite or common effects on different saccade types. *Experimental Brain Research*, 155, 231–244. <http://dx.doi.org/10.1007/s00221-003-1717-9>
- Kristjánsson, A., Vuilleumier, P., Schwartz, S., Macaluso, E., & Driver, J. (2007). Neural basis for priming of pop-out during visual search revealed with fMRI. *Cerebral Cortex*, 17, 1612–1624. <http://dx.doi.org/10.1093/cercor/bhl072>
- Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature*, 384, 74–77. <http://dx.doi.org/10.1038/384074a0>
- Kusunoki, M., Gottlieb, J., & Goldberg, M. E. (2000). The lateral intraparietal area as a salience map: The representation of abrupt onset, stimulus motion, and task relevance. *Vision Research*, 40, 1459–1468. [http://dx.doi.org/10.1016/S0042-6989\(99\)00212-6](http://dx.doi.org/10.1016/S0042-6989(99)00212-6)
- LaBerge, D. (1990). Thalamic and cortical mechanisms of attention suggested by recent positron emission tomographic experiments. *Journal of Cognitive Neuroscience*, 2, 358–372. <http://dx.doi.org/10.1162/jocn.1990.2.4.358>
- LaBerge, D. (2002). Attentional control: Brief and prolonged. *Psychological Research*, 66, 220–233. <http://dx.doi.org/10.1007/s00426-002-0097-2>
- Lambert, A., Naikar, N., McLachlan, K., & Aitken, V. (1999). A new component of visual orienting: Implicit effects of peripheral information and subthreshold cues on covert attention. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 321–340. <http://dx.doi.org/10.1037/0096-1523.25.2.321>
- Leh, S. E., Johansen-Berg, H., & Ptito, A. (2006). Unconscious vision: New insights into the neuronal correlate of blindsight using diffusion tractography. *Brain: A Journal of Neurology*, 129, 1822–1832. <http://dx.doi.org/10.1093/brain/awl111>
- Leh, S. E., Mullen, K. T., & Ptito, A. (2006). Absence of S-cone input in human blindsight following hemispherectomy. *European Journal of Neuroscience*, 24, 2954–2960. <http://dx.doi.org/10.1111/j.1460-9568.2006.05178.x>
- Leh, S. E., Ptito, A., Schönwiesner, M., Chakravarty, M. M., & Mullen, K. T. (2010). Blindsight mediated by an S-cone-independent collicular pathway: An fMRI study in hemispherectomized subjects. *Journal of Cognitive Neuroscience*, 22, 670–682. <http://dx.doi.org/10.1162/jocn.2009.21217>
- Leopold, D. A. (2012). Primary visual cortex: Awareness and blindsight. *Annual Review of Neuroscience*, 35, 91–109. <http://dx.doi.org/10.1146/annurev-neuro-062111-150356>
- Lewis, T. L., Maurer, D., & Blackburn, K. (1985). The development of young infants’ ability to detect stimuli in the nasal visual field. *Vision Research*, 25, 943–950. [http://dx.doi.org/10.1016/0042-6989\(85\)90205-6](http://dx.doi.org/10.1016/0042-6989(85)90205-6)
- Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., . . . Williams, L. M. (2005). A direct brainstem-amygdala-cortical ‘alarm’ system for subliminal signals of fear. *NeuroImage*, 24, 235–243. <http://dx.doi.org/10.1016/j.neuroimage.2004.08.016>
- Lin, Z., & He, S. (2009). Seeing the invisible: The scope and limits of unconscious processing in binocular rivalry. *Progress in Neurobiology*, 87, 195–211. <http://dx.doi.org/10.1016/j.pneurobio.2008.09.002>
- Ling, S., & Blake, R. (2012). Normalization regulates competition for visual awareness. *Neuron*, 75, 531–540. <http://dx.doi.org/10.1016/j.neuron.2012.05.032>
- Ling, S., Pratte, M. S., & Tong, F. (2015). Attention alters orientation processing in the human lateral geniculate nucleus. *Nature Neuroscience*, 18, 496–498. <http://dx.doi.org/10.1038/nn.3967>
- Lovejoy, L. P., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nature Neuroscience*, 13, 261–266. <http://dx.doi.org/10.1038/nn.2470>
- Lyon, D. C., Nassi, J. J., & Callaway, E. M. (2010). A disynaptic relay from superior colliculus to dorsal stream visual cortex in macaque monkey. *Neuron*, 65, 270–279. <http://dx.doi.org/10.1016/j.neuron.2010.01.003>
- Machado, L., & Rafal, R. D. (2004a). Control of fixation and saccades during an anti-saccade task: An investigation in humans with chronic lesions of oculomotor cortex. *Experimental Brain Research*, 156, 55–63. <http://dx.doi.org/10.1007/s00221-003-1765-1>
- Machado, L., & Rafal, R. D. (2004b). Control of fixation and saccades in humans with chronic lesions of oculomotor cortex. *Neuropsychology*, 18, 115–123. <http://dx.doi.org/10.1037/0894-4105.18.1.115>
- Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neuroscience*, 1, 144–149. <http://dx.doi.org/10.1038/393>
- MacLeod, D. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America*, 69, 1183–1186. <http://dx.doi.org/10.1364/JOSA.69.001183>
- Marrocco, R. T., & Li, R. H. (1977). Monkey superior colliculus: Properties of single cells and their afferent inputs. *Journal of Neurophysiology*, 40, 844–860.
- McAlonan, K., Cavanaugh, J., & Wurtz, R. H. (2008). Guarding the gateway to cortex with attention in visual thalamus. *Nature*, 456, 391–394. <http://dx.doi.org/10.1038/nature07382>

- McCormick, P. A. (1997). Orienting attention without awareness. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 168–180. <http://dx.doi.org/10.1037/0096-1523.23.1.168>
- Mele, S., Savazzi, S., Marzi, C. A., & Berlucchi, G. (2008). Reaction time inhibition from subliminal cues: Is it related to inhibition of return? *Neuropsychologia*, 46, 810–819. <http://dx.doi.org/10.1016/j.neuropsychologia.2007.11.003>
- Michael, G. A., Boucart, M., Degreef, J. F., & Godefroy, O. (2001). The thalamus interrupts top-down attentional control for permitting exploratory shiftings to sensory signals. *Neuroreport*, 12, 2041–2048. <http://dx.doi.org/10.1097/00001756-200107030-00050>
- Michael, G. A., & Buron, V. (2005). The human pulvinar and stimulus-driven attentional control. *Behavioral Neuroscience*, 119, 1353–1367. <http://dx.doi.org/10.1037/0735-7044.119.5.1353>
- Michael, G. A., & Desmedt, S. (2004). The human pulvinar and attentional processing of visual distractors. *Neuroscience Letters*, 362, 176–181. <http://dx.doi.org/10.1016/j.neulet.2004.01.062>
- Michael, G. A., & Gálvez-García, G. (2011). Saliency-based progression of visual attention. *Behavioural Brain Research*, 224, 87–99. <http://dx.doi.org/10.1016/j.bbr.2011.05.024>
- Michael, G. A., Mizzi, R., Couffe, C., Gálvez-García, G., & Labeye, E. (2016). Spotting from the rightmost deep: Right hemisphere extrageniculate mediation in filtering out distractors revealed by a temporal field advantage. *AIMS Neuroscience*, 3, 56–66. <http://dx.doi.org/10.3934/Neuroscience.2016.1.56>
- Michael, G. A., & Ojeda, N. (2005). Visual field asymmetries in selective attention: Evidence from a modified search paradigm. *Neuroscience Letters*, 388, 65–70. <http://dx.doi.org/10.1016/j.neulet.2005.06.027>
- Mizuno, N., Itoh, K., Uchida, K., Uemura-Sumi, M., & Matsushima, R. (1982). A retino-pulvinar projection in the macaque monkey as visualized by the use of anterograde transport of horseradish peroxidase. *Neuroscience Letters*, 30, 199–203. [http://dx.doi.org/10.1016/0304-3940\(82\)90399-8](http://dx.doi.org/10.1016/0304-3940(82)90399-8)
- Mizzi, R., & Michael, G. A. (2014). The role of the collicular pathway in the saliency-based progression of visual attention. *Behavioural Brain Research*, 270, 330–338. <http://dx.doi.org/10.1016/j.bbr.2014.05.043>
- Mollon, J. D., & Polden, P. G. (1975). Colour illusion and evidence for interaction between cone mechanisms. *Nature*, 258, 421–422. <http://dx.doi.org/10.1038/258421a0>
- Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, 40, 671–683. [http://dx.doi.org/10.1016/S0896-6273\(03\)00716-5](http://dx.doi.org/10.1016/S0896-6273(03)00716-5)
- Morris, J. S., Öhman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 1680–1685. <http://dx.doi.org/10.1073/pnas.96.4.1680>
- Mulckhuyse, M., & Theeuwes, J. (2010a). Unconscious attentional orienting to exogenous cues: A review of the literature. *Acta Psychologica*, 134, 299–309. <http://dx.doi.org/10.1016/j.actpsy.2010.03.002>
- Mulckhuyse, M., & Theeuwes, J. (2010b). Unconscious cueing effects in saccadic eye movements—Facilitation and inhibition in temporal and nasal hemifield. *Vision Research*, 50, 606–613. <http://dx.doi.org/10.1016/j.visres.2010.01.005>
- Müri, R. M., Rivaud, S., Gaymard, B., Ploner, C. J., Vermersch, A. I., Hess, C. W., & Pierrot-Deseilligny, C. (1998). Role of the prefrontal cortex in the control of express saccades. A transcranial magnetic stimulation study. *Neuropsychologia*, 37, 199–206. [http://dx.doi.org/10.1016/S0028-3932\(98\)00094-3](http://dx.doi.org/10.1016/S0028-3932(98)00094-3)
- Nakagawa, S., & Tanaka, S. (1984). Retinal projections to the pulvinar nucleus of the macaque monkey: A re-investigation using autoradiography. *Experimental Brain Research*, 57, 151–157. <http://dx.doi.org/10.1007/BF00231141>
- O’Brien, B. J., Abel, P. L., & Olavarria, J. F. (2001). The retinal input to calbindin-D28k-defined subdivisions in macaque inferior pulvinar. *Neuroscience Letters*, 312, 145–148. [http://dx.doi.org/10.1016/S0304-3940\(01\)02220-0](http://dx.doi.org/10.1016/S0304-3940(01)02220-0)
- O’Connor, D. H., Fukui, M. M., Pinsk, M. A., & Kastner, S. (2002). Attention modulates responses in the human lateral geniculate nucleus. *Nature Neuroscience*, 5, 1203–1209. <http://dx.doi.org/10.1038/nn957>
- Oke, A., Keller, R., Mefford, I., & Adams, R. N. (1978). Lateralization of norepinephrine in human thalamus. *Science*, 200, 1411–1413. <http://dx.doi.org/10.1126/science.663623>
- Osterberg, G. (1935). Topography of the layer of rods and cones in the human retina. *Acta Ophthalmologica*, 6(Suppl.), 1–103.
- Overgaard, M. (2012). Blindsight: Recent and historical controversies on the blindness of blindsight. *Wiley Interdisciplinary Reviews: Cognitive Science*, 3, 607–614. <http://dx.doi.org/10.1002/wcs.1194>
- Palmer, S., & Mattler, U. (2013a). Masked stimuli modulate endogenous shifts of spatial attention. *Consciousness and Cognition*, 22, 486–503. <http://dx.doi.org/10.1016/j.concog.2013.02.008>
- Palmer, S., & Mattler, U. (2013b). On the source and scope of priming effects of masked stimuli on endogenous shifts of spatial attention. *Consciousness and Cognition*, 22, 528–544. <http://dx.doi.org/10.1016/j.concog.2013.03.002>
- Pardo, J. V., Fox, P. T., & Raichle, M. E. (1991). Localization of a human system for sustained attention by positron emission tomography. *Nature*, 349, 61–64. <http://dx.doi.org/10.1038/349061a0>
- Perry, V. H., & Cowey, A. (1984). Retinal ganglion cells that project to the superior colliculus and pretectum in the macaque monkey. *Neuroscience*, 12, 1125–1137. [http://dx.doi.org/10.1016/0306-4522\(84\)90007-1](http://dx.doi.org/10.1016/0306-4522(84)90007-1)
- Petersen, S. E., Robinson, D. L., & Keys, W. (1985). Pulvinar nuclei of the behaving rhesus monkey: Visual responses and their modulation. *Journal of Neurophysiology*, 54, 867–886.
- Petersen, S. E., Robinson, D. L., & Morris, J. D. (1987). Contributions of the pulvinar to visual spatial attention. *Neuropsychologia*, 25, 97–105. [http://dx.doi.org/10.1016/0028-3932\(87\)90046-7](http://dx.doi.org/10.1016/0028-3932(87)90046-7)
- Ploner, C. J., Gaymard, B. M., Rivaud-Péchoux, S., & Pierrot-Deseilligny, C. (2005). The prefrontal substrate of reflexive saccade inhibition in humans. *Biological Psychiatry*, 57, 1159–1165. <http://dx.doi.org/10.1016/j.biopsych.2005.02.017>
- Pollack, J. G., & Hickey, T. L. (1979). The distribution of retino-collicular axon terminals in rhesus monkey. *The Journal of Comparative Neurology*, 185, 587–602. <http://dx.doi.org/10.1002/cne.901850402>
- Posner, M. I., & Cohen, Y. (1980). Attention and the control of movements. In G. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior I* (pp. 243–248). Amsterdam, North-Holland: Elsevier. [http://dx.doi.org/10.1016/S0166-4115\(08\)61949-4](http://dx.doi.org/10.1016/S0166-4115(08)61949-4)
- Posner, M. I., Cohen, Y., & Rafal, R. D. (1982). Neural systems control of spatial orienting. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 298, 187–198. <http://dx.doi.org/10.1098/rstb.1982.0081>
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, 13, 25–42. <http://dx.doi.org/10.1146/annurev.ne.13.030190.000325>
- Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, 14, 619–633. <http://dx.doi.org/10.1093/cercor/bbh023>
- Purushothaman, G., Marion, R., Li, K., & Casagrande, V. A. (2012). Gating and control of primary visual cortex by pulvinar. *Nature Neuroscience*, 15, 905–912. <http://dx.doi.org/10.1038/nn.3106>
- Rafal, R. D. (2006). Oculomotor functions of the parietal lobe: Effects of chronic lesions in humans. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior*, 42, 730–739.
- Rafal, R., Henik, A., & Smith, J. (1991). Extrageniculate contributions to reflex visual orienting in normal humans: A temporal hemifield advantage. *Journal of Cognitive Neuroscience*, 3, 322–328. <http://dx.doi.org/10.1162/jocn.1991.3.4.322>

- Rafal, R. D., Inhoff, A. W., Friedman, J. H., & Bernstein, E. (1987). Programming and execution of sequential movements in Parkinson's disease. *Journal of Neurology, Neurosurgery, and Psychiatry*, 50, 1267–1273. <http://dx.doi.org/10.1136/jnnp.50.10.1267>
- Rafal, R. D., Machado, L., & Ingle, H. (2000). Looking forward to looking: Saccade preparation and control of the visual grasp reflex. In S. Monsell & J. Driver (Eds.), *Control of cognitive processes: Attention and performance* (Vol. XVIII, pp. 155–174). Cambridge, UK: MIT Press.
- Rafal, R. D., Posner, M. I., Friedman, J. H., Inhoff, A. W., & Bernstein, E. (1988). Orienting of visual attention in progressive supranuclear palsy. *Brain: A Journal of Neurology*, 111, 267–280. <http://dx.doi.org/10.1093/brain/111.2.267>
- Rafal, R., Smith, J., Krantz, J., Cohen, A., & Brennan, C. (1990). Extrageniculate vision in hemianopic humans: Saccade inhibition by signals in the blind field. *Science*, 250, 118–121. <http://dx.doi.org/10.1126/science.2218503>
- Rao, Y., & Wu, J. Y. (2001). Neuronal migration and the evolution of the human brain. *Nature Neuroscience*, 4, 860–862. <http://dx.doi.org/10.1038/nn0901-860>
- Ratcliff, R., & Rouder, J. N. (1998). Modeling response times for two-choice decisions. *Psychological Science*, 9, 347–356. <http://dx.doi.org/10.1111/1467-9280.00067>
- Reuss, H., Kiesel, A., Kunde, W., & Wühr, P. (2012). A cue from the unconscious - masked symbols prompt spatial anticipation. *Frontiers in Psychology*, 3, 397. <http://dx.doi.org/10.3389/fpsyg.2012.00397>
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25, 31–40. [http://dx.doi.org/10.1016/0028-3932\(87\)90041-8](http://dx.doi.org/10.1016/0028-3932(87)90041-8)
- Robinson, D. L., & McClurkin, J. W. (1989). The visual superior colliculus and pulvinar. *Reviews of Oculomotor Research*, 3, 337–360.
- Robinson, D. L., & Petersen, S. E. (1992). The pulvinar and visual salience. *Trends in Neurosciences*, 15, 127–132. [http://dx.doi.org/10.1016/0166-2236\(92\)90354-B](http://dx.doi.org/10.1016/0166-2236(92)90354-B)
- Rodieke, R. W., & Watanabe, M. (1993). Survey of the morphology of macaque retinal ganglion cells that project to the pretectum, superior colliculus, and parvicellular laminae of the lateral geniculate nucleus. *The Journal of Comparative Neurology*, 338, 289–303. <http://dx.doi.org/10.1002/cne.903380211>
- Roseboom, W., & Arnold, D. H. (2011). Learning to reach for 'invisible' visual input. *Current Biology*, 21, R493–R494. <http://dx.doi.org/10.1016/j.cub.2011.05.036>
- Rothbart, M. K., Posner, M. I., & Boylan, A. (1990). Regulatory mechanisms in infant development. In J. T. Enns (Ed.), *Advances in psychology* (Vol. 69, pp. 47–66). North-Holland, the Netherlands: Elsevier. Retrieved from <http://www.sciencedirect.com/science/article/pii/S016641508604501>
- Rothkirch, M., Stein, T., Sekutowicz, M., & Sterzer, P. (2012). A direct oculomotor correlate of unconscious visual processing. *Current Biology*, 22, R514–R515. <http://dx.doi.org/10.1016/j.cub.2012.04.046>
- Rotshtein, P., Soto, D., Greucci, A., Geng, J. J., & Humphreys, G. W. (2011). The role of the pulvinar in resolving competition between memory and visual selection: A functional connectivity study. *Neuropsychologia*, 49, 1544–1552. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.002>
- Saalmann, Y. B., & Kastner, S. (2011). Cognitive and perceptual functions of the visual thalamus. *Neuron*, 71, 209–223. <http://dx.doi.org/10.1016/j.neuron.2011.06.027>
- Sahibzada, N., Dean, P., & Redgrave, P. (1986). Movements resembling orientation or avoidance elicited by electrical stimulation of the superior colliculus in rats. *The Journal of Neuroscience*, 6, 723–733.
- Sahraie, A., Weiskrantz, L., Barbur, J. L., Simmons, A., Williams, S. C. R., & Brammer, M. J. (1997). Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 9406–9411. <http://dx.doi.org/10.1073/pnas.94.17.9406>
- Sapir, A., Rafal, R., & Henik, A. (2002). Attending to the thalamus: Inhibition of return and nasal-temporal asymmetry in the pulvinar. *Neuroreport*, 13, 693–697. <http://dx.doi.org/10.1097/00001756-200204160-00031>
- Sapir, A., Soroker, N., Berger, A., & Henik, A. (1999). Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nature Neuroscience*, 2, 1053–1054. <http://dx.doi.org/10.1038/15977>
- Schiller, P. H. (1968). Single unit analysis of backward visual masking and metacontrast in the cat lateral geniculate nucleus. *Vision Research*, 8, 855–866. [http://dx.doi.org/10.1016/0042-6989\(68\)90135-1](http://dx.doi.org/10.1016/0042-6989(68)90135-1)
- Schiller, P. H., & Malpeli, J. G. (1977). Properties and tectal projections of monkey retinal ganglion cells. *Journal of Neurophysiology*, 40, 428–445.
- Schmid, M. C., Mrowka, S. W., Turchi, J., Saunders, R. C., Wilke, M., Peters, A. J., . . . Leopold, D. A. (2010). Blindsight depends on the lateral geniculate nucleus. *Nature*, 466, 373–377. <http://dx.doi.org/10.1038/nature09179>
- Schneider, K. A. (2011). Subcortical mechanisms of feature-based attention in the human brain. *The Journal of Neuroscience*, 31, 8643–8653. <http://dx.doi.org/10.1523/JNEUROSCI.6274-10.2011>
- Schneider, K. A., & Kastner, S. (2005). Visual responses of the human superior colliculus: A high-resolution functional magnetic resonance imaging study. *Journal of Neurophysiology*, 94, 2491–2503. <http://dx.doi.org/10.1152/jn.00288.2005>
- Schneider, K. A., & Kastner, S. (2009). Effects of sustained spatial attention in the human lateral geniculate nucleus and superior colliculus. *The Journal of Neuroscience*, 29, 1784–1795. <http://dx.doi.org/10.1523/JNEUROSCI.4452-08.2009>
- Shen, K., Valero, J., Day, G. S., & Paré, M. (2011). Investigating the role of the superior colliculus in active vision with the visual search paradigm. *European Journal of Neuroscience*, 33, 2003–2016. <http://dx.doi.org/10.1111/j.1460-9568.2011.07722.x>
- Shipp, S. (2004). The brain circuitry of attention. *Trends in Cognitive Sciences*, 8, 223–230. <http://dx.doi.org/10.1016/j.tics.2004.03.004>
- Shulman, G. L. (1984). An asymmetry in the control of eye movements and shifts of attention. *Acta Psychologica*, 55, 53–69. [http://dx.doi.org/10.1016/0001-6918\(84\)90059-3](http://dx.doi.org/10.1016/0001-6918(84)90059-3)
- Slater, A. M., & Findlay, J. M. (1972). The measurement of fixation position in the newborn baby. *Journal of Experimental Child Psychology*, 14, 349–364. [http://dx.doi.org/10.1016/0022-0965\(72\)90056-2](http://dx.doi.org/10.1016/0022-0965(72)90056-2)
- Smithson, H. E. (2014). S-cone psychophysics. *Visual Neuroscience*, 31, 211–225. <http://dx.doi.org/10.1017/S0952523814000030>
- Smithson, H. E., Bourke, A., Zaidi, Q., Mollon, J. D., & Stockman, A. (2004). Three ways to find a tritan line. *Journal of Vision*, 4, 83. <http://dx.doi.org/10.1167/4.11.83>
- Smithson, H. E., & Mollon, J. D. (2004). Is the S-opponent chromatic sub-system sluggish? *Vision Research*, 44, 2919–2929. <http://dx.doi.org/10.1016/j.visres.2004.06.022>
- Smithson, H. E., Sumner, P., & Mollon, J. D. (2003). How to find a tritan line. In J. D. Mollon, J. Pokorny, & K. Knoblauch (Eds.), *Normal and defective colour vision* (pp. 279–287). New York, NY: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780198525301.003.0029>
- Snow, J. C., Allen, H. A., Rafal, R. D., & Humphreys, G. W. (2009). Impaired attentional selection following lesions to human pulvinar: Evidence for homology between human and monkey. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 4054–4059. <http://dx.doi.org/10.1073/pnas.0810086106>
- Sommer, M. A., & Wurtz, R. H. (2000). Composition and topographic organization of signals sent from the frontal eye field to the superior colliculus. *Journal of Neurophysiology*, 83, 1979–2001.

- Spring, M., & Carrasco, M. (2015). Acting without seeing: Eye movements reveal visual processing without awareness. *Trends in Neurosciences*, 38, 247–258. <http://dx.doi.org/10.1016/j.tins.2015.02.002>
- Spring, M., Pomplun, M., & Carrasco, M. (2011). Tracking without perceiving: A dissociation between eye movements and motion perception. *Psychological Science*, 22, 216–225. <http://dx.doi.org/10.1177/0956797610394659>
- Sterzer, P., Stein, T., Ludwig, K., Rothkirch, M., & Hesselmann, G. (2014). Neural processing of visual information under interocular suppression: A critical review. *Frontiers in Psychology*, 5, 453. <http://dx.doi.org/10.3389/fpsyg.2014.00453>
- Stockman, A., MacLeod, D. I., & DePriest, D. D. (1991). The temporal properties of the human short-wave photoreceptors and their associated pathways. *Vision Research*, 31, 189–208. [http://dx.doi.org/10.1016/0042-6989\(91\)90111-H](http://dx.doi.org/10.1016/0042-6989(91)90111-H)
- Stockman, A., MacLeod, D. I., & Lebrun, S. J. (1993). Faster than the eye can see: Blue cones respond to rapid flicker. *Journal of the Optical Society of America A, Optics and Image Science*, 10, 1396–1402. <http://dx.doi.org/10.1364/JOSAA.10.001396>
- Stoerig, P., & Cowey, A. (1997). Blindsight in man and monkey. *Brain: A Journal of Neurology*, 120, 535–559. <http://dx.doi.org/10.1093/brain/120.3.535>
- Strumpf, H., Mangun, G. R., Boehler, C. N., Stoppel, C., Schoenfeld, M. A., Heinze, H.-J., & Hopf, J.-M. (2013). The role of the pulvinar in distractor processing and visual search. *Human Brain Mapping*, 34, 1115–1132. <http://dx.doi.org/10.1002/hbm.21496>
- Sumner, P., Adamjee, T., & Mollon, J. D. (2002). Signals invisible to the collicular and magnocellular pathways can capture visual attention. *Current Biology*, 12, 1312–1316. [http://dx.doi.org/10.1016/S0960-9822\(02\)01020-5](http://dx.doi.org/10.1016/S0960-9822(02)01020-5)
- Sumner, P., Nachev, P., Castor-Perry, S., Isenman, H., & Kennard, C. (2006). Which visual pathways cause fixation-related inhibition? *Journal of Neurophysiology*, 95, 1527–1536. <http://dx.doi.org/10.1152/jn.00781.2005>
- Sumner, P., Nachev, P., Vora, N., Husain, M., & Kennard, C. (2004). Distinct cortical and collicular mechanisms of inhibition of return revealed with S cone stimuli. *Current Biology*, 14, 2259–2263. <http://dx.doi.org/10.1016/j.cub.2004.12.021>
- Sylvester, R., Josephs, O., Driver, J., & Rees, G. (2007). Visual fMRI responses in human superior colliculus show a temporal-nasal asymmetry that is absent in lateral geniculate and visual cortex. *Journal of Neurophysiology*, 97, 1495–1502. <http://dx.doi.org/10.1152/jn.00835.2006>
- Tamietto, M., Cauda, F., Corazzini, L. L., Savazzi, S., Marzi, C. A., Goebel, R., . . . de Gelder, B. (2010). Collicular vision guides nonconscious behavior. *Journal of Cognitive Neuroscience*, 22, 888–902. <http://dx.doi.org/10.1162/jocn.2009.21225>
- Tamietto, M., Pullens, P., de Gelder, B., Weiskrantz, L., & Goebel, R. (2012). Subcortical connections to human amygdala and changes following destruction of the visual cortex. *Current Biology*, 22, 1449–1455. <http://dx.doi.org/10.1016/j.cub.2012.06.006>
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, 10, 502–511. <http://dx.doi.org/10.1016/j.tics.2006.09.003>
- Troiani, V., & Schultz, R. T. (2013). Amygdala, pulvinar, and inferior parietal cortex contribute to early processing of faces without awareness. *Frontiers in Human Neuroscience*, 7, 241. <http://dx.doi.org/10.3389/fnhum.2013.00241>
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8, 1096–1101. <http://dx.doi.org/10.1038/nn1500>
- Van der Stigchel, S., Mulckhuyse, M., & Theeuwes, J. (2009). Eye cannot see it: The interference of subliminal distractors on saccade metrics. *Vision Research*, 49, 2104–2109. <http://dx.doi.org/10.1016/j.visres.2009.05.018>
- Vidal, J. R., Chaumon, M., O'Regan, J. K., & Tallon-Baudry, C. (2006). Visual grouping and the focusing of attention induce gamma-band oscillations at different frequencies in human magnetoencephalogram signals. *Journal of Cognitive Neuroscience*, 18, 1850–1862. <http://dx.doi.org/10.1162/jocn.2006.18.11.1850>
- Villeneuve, M. Y., Kupers, R., Gjedde, A., Ptito, M., & Casanova, C. (2005). Pattern-motion selectivity in the human pulvinar. *NeuroImage*, 28, 474–480. <http://dx.doi.org/10.1016/j.neuroimage.2005.06.015>
- Vuilleumier, P., & Schwartz, S. (2001). Beware and be aware: Capture of spatial attention by fear-related stimuli in neglect. *NeuroReport*, 12, 1119–1122. <http://dx.doi.org/10.1097/00001756-200105080-00014>
- Walker, R., Mannan, S., Maurer, D., Pambakian, A. L., & Kennard, C. (2000). The oculomotor distractor effect in normal and hemianopic vision. *Proceedings Biological Sciences*, 267, 431–438. <http://dx.doi.org/10.1098/rspb.2000.1018>
- Wang, J., & Wade, A. R. (2011). Differential attentional modulation of cortical responses to S-cone and luminance stimuli. *Journal of Vision*, 11, 1. <http://dx.doi.org/10.1167/11.6.1>
- Wässle, H., & Boycott, B. B. (1991). Functional architecture of the mammalian retina. *Physiological Reviews*, 71, 447–480.
- Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., & Logothetis, N. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science*, 334, 829–831. <http://dx.doi.org/10.1126/science.1203161>
- Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. *Vision Research*, 34, 1993–2020. [http://dx.doi.org/10.1016/0042-6989\(94\)90028-0](http://dx.doi.org/10.1016/0042-6989(94)90028-0)
- Weiskrantz, L. (1986). *Blindsight: A case study and its implications*. New York, NY: Oxford University Press. Retrieved from <http://www.oxfordscholarship.com/view/10.1093/acprof:oso/9780198521921.001.0001/acprof-9780198521921>
- Weiskrantz, L. (2009). Is blindsight just degraded normal vision? *Experimental Brain Research*, 192, 413–416. <http://dx.doi.org/10.1007/s00221-008-1388-7>
- Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron*, 39, 1043–1052. <http://dx.doi.org/10.1016/j.neuron.2003.08.003>
- Wilke, M., Mueller, K.-M., & Leopold, D. A. (2009). Neural activity in the visual thalamus reflects perceptual suppression. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 9465–9470. <http://dx.doi.org/10.1073/pnas.0900714106>
- Williams, C., Azzopardi, P., & Cowey, A. (1995). Nasal and temporal retinal ganglion cells projecting to the midbrain: Implications for “blindsight”. *Neuroscience*, 65, 577–586. [http://dx.doi.org/10.1016/0306-4522\(94\)00489-R](http://dx.doi.org/10.1016/0306-4522(94)00489-R)
- Wilson, M. E., & Toyne, M. J. (1970). Retino-tectal and cortico-tectal projections in *Macaca mulatta*. *Brain Research*, 24, 395–406. [http://dx.doi.org/10.1016/0006-8993\(70\)90181-2](http://dx.doi.org/10.1016/0006-8993(70)90181-2)
- Wunderlich, K., Schneider, K. A., & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience*, 8, 1595–1602. <http://dx.doi.org/10.1038/nn1554>
- Wurtz, R. H., McAlonan, K., Cavanaugh, J., & Berman, R. A. (2011). Thalamic pathways for active vision. *Trends in Cognitive Sciences*, 15, 177–184. <http://dx.doi.org/10.1016/j.tics.2011.02.004>
- Wyszecki, G., & Stiles, W. S. (1982). *Color science* (Vol. 8). New York, NY: Wiley-Blackwell.
- Xu, S., Zhang, S., & Geng, H. (2011). Gaze-induced joint attention persists under high perceptual load and does not depend on awareness. *Vision Research*, 51, 2048–2056. <http://dx.doi.org/10.1016/j.visres.2011.07.023>
- Yoshida, M., Itti, L., Berg, D. J., Ikeda, T., Kato, R., Takaura, K., . . . Isa, T. (2012). Residual attention guidance in blindsight monkeys watching

- complex natural scenes. *Current Biology*, 22, 1429–1434. <http://dx.doi.org/10.1016/j.cub.2012.05.046>
- Yuval-Greenberg, S., & Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *The Journal of Neuroscience*, 33, 9635–9643. <http://dx.doi.org/10.1523/JNEUROSCI.4612-12.2013>
- Zackon, D. H., Casson, E. J., Stelmach, L., Faubert, J., & Racette, L. (1997). Distinguishing subcortical and cortical influences in visual attention. Subcortical attentional processing. *Investigative Ophthalmology & Visual Science*, 38, 364–371.
- Zackon, D. H., Casson, E. J., Zafar, A., Stelmach, L., & Racette, L. (1999). The temporal order judgment paradigm: Subcortical attentional contribution under exogenous and endogenous cueing conditions. *Neuropsychologia*, 37, 511–520. [http://dx.doi.org/10.1016/S0028-3932\(98\)00134-1](http://dx.doi.org/10.1016/S0028-3932(98)00134-1)
- Zhang, P., Jamison, K., Engel, S., He, B., & He, S. (2011). Binocular rivalry requires visual attention. *Neuron*, 71, 362–369. <http://dx.doi.org/10.1016/j.neuron.2011.05.035>

Received November 6, 2015

Revision received May 25, 2016

Accepted June 14, 2016 ■

Members of Underrepresented Groups: Reviewers for Journal Manuscripts Wanted

If you are interested in reviewing manuscripts for APA journals, the APA Publications and Communications Board would like to invite your participation. Manuscript reviewers are vital to the publications process. As a reviewer, you would gain valuable experience in publishing. The P&C Board is particularly interested in encouraging members of underrepresented groups to participate more in this process.

If you are interested in reviewing manuscripts, please write APA Journals at Reviewers@apa.org. Please note the following important points:

- To be selected as a reviewer, you must have published articles in peer-reviewed journals. The experience of publishing provides a reviewer with the basis for preparing a thorough, objective review.
- To be selected, it is critical to be a regular reader of the five to six empirical journals that are most central to the area or journal for which you would like to review. Current knowledge of recently published research provides a reviewer with the knowledge base to evaluate a new submission within the context of existing research.
- To select the appropriate reviewers for each manuscript, the editor needs detailed information. Please include with your letter your vita. In the letter, please identify which APA journal(s) you are interested in, and describe your area of expertise. Be as specific as possible. For example, “social psychology” is not sufficient—you would need to specify “social cognition” or “attitude change” as well.
- Reviewing a manuscript takes time (1–4 hours per manuscript reviewed). If you are selected to review a manuscript, be prepared to invest the necessary time to evaluate the manuscript thoroughly.

APA now has an online video course that provides guidance in reviewing manuscripts. To learn more about the course and to access the video, visit <http://www.apa.org/pubs/authors/review-manuscript-ce-video.aspx>.