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Tuning the Senses: How the Pupil Shapes Vision at the Earliest Stage

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Keywords

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Abstract

The pupil responds reflexively to changes in brightness and focal distance to maintain the smallest pupil (and thus the highest visual acuity) that still allows sufficient light to reach the retina. The pupil also responds to a wide variety of cognitive processes, but the functions of these cognitive responses are still poorly understood. In this review, I propose that cognitive pupil responses, like their reflexive counterparts, serve to optimize vision. Specifically, an emphasis on central vision over peripheral vision results in pupil constriction, and this likely reflects the fact that central vision benefits most from the increased visual acuity provided by small pupils. Furthermore, an intention to act with a bright stimulus results in preparatory pupil constriction, which allows the pupil to respond quickly when that bright stimulus is subsequently brought into view. More generally, cognitively driven pupil responses are likely a form of sensory tuning: a subtle adjustment of the eyes to optimize their properties for the current situation and the immediate future.

1. INTRODUCTION

Vision scientists traditionally distinguish perception from sensation. Perception refers to the brain's interpretation of sensory input and as such would be affected by cognitive factors such as prediction, attention, and reward. In contrast, sensation refers to how (photo)receptors respond to sensory input and as such would be unaffected by cognition. But how independent is visual sensation from cognition, really?

The key tenet of this review is that we actively tune our senses, and specifically our eyes, to optimize their properties for the current situation and the immediate future. Saccadic eye movements are a familiar example of this: We shift our gaze to bring relevant information into central vision (Kowler 2011). This allows us to sense relevant information with the central part of the retina, which contains a dense network of cone photoreceptors that provides high-acuity vision (Curcio et al. 1987).

However, the muscles of the eye allow for many more movements than only those that shift gaze in space. For example, the curvature of the lens can increase (accommodation) to shift the point of focus from far to near (Brown 1973). The eyes can rotate clockwise or counterclockwise (when viewed from the front); such torsional eye movements may serve little purpose in humans or other animals with frontally placed eyes, but they stabilize gaze in animals with lateral eyes (Banks et al. 2015). In total, the eye is controlled by fourteen muscles: six that rotate the eye, five that control the eyelid, one that controls lens accommodation, and two that control pupil size; together, these muscles provide the eye with an incredible freedom of movement and shape.

In this review, I focus on pupil responses, which profoundly affect how visual information falls onto the retina. I start by introducing the three main factors that cause the pupil to constrict (become smaller) or dilate (become bigger): light, focal distance, and arousal (Section 2). I then describe how pupil size is related to visual cognition, with a focus on visual attention, working memory, and mental imagery (Section 3), and also how pupil size is related to eye movements (Section 4). Following that, I describe how pupil responses affect the way that light falls onto the retina, which in turn affects the way that visual input is processed by visual brain areas, which in turn affects visually guided behavior and subjective visual experience (Section 5). Finally, I outline a general theory of sensory tuning based on the findings reviewed in this article; this theory focuses on vision and pupil size, but I end by proposing that sensory tuning is a general principle of sensation and perception.

2. PUPIL RESPONSES

There are three broad classes of pupil responses. These differ primarily in the stimulus that triggers the response, but they are also controlled by partially distinct neural pathways (for a detailed discussion, see Mathôt 2018).

2.1. The Pupil Light Response

When you walk from a shady office into the bright outdoors, your pupils rapidly constrict; this is the pupil light response (PLR), a large response that can change the pupil from its maximum (± 8 mm in humans) to its minimum size (± 2 mm in humans), thus changing the amount of light that enters the eye by a factor of roughly 16. Following exposure to light, the pupil starts to constrict with a latency of 200–250 ms (Ellis 1981), reaching its minimum size after roughly 1,000–2,000 ms (the exact latencies depend mostly on the strength of the stimulus). This initial constriction is ballistic in the sense that it occurs even in response to very brief flashes of light,

in which case the pupil starts to constrict only after the light has already been extinguished. The initial constriction is driven largely by rods and cones, the same photoreceptors that also mediate regular (image-forming) vision; consequently, the initial constriction has many of the same properties as regular vision, including a fast response profile that is dominated by input from central vision (Crawford 1936, Hong et al. 2001).

Rods and cones respond vigorously to changes in brightness but quickly adapt when brightness remains constant (Nakatani & Yau 1988). Therefore, if the PLR were only driven by rods and cones, then increases in brightness would cause a transient pupil constriction, but this constriction would not be maintained. The fact that pupils can stay constricted indefinitely is due to a different class of photoreceptors: intrinsically photosensitive retinal ganglion cells (ipRGCs) (for a review, see Do 2019). Like regular retinal ganglion cells, ipRGCs receive input from rods and cones. However, they are also photosensitive themselves through a photopigment called melanopsin. The melanopsin response is slow, with a latency of up to 10 s, does not show adaptation, and has a peak sensitivity to bluish light, somewhat in between the peak sensitivities of rods and S (blue) cones (Markwell et al. 2010). This melanopsin response is what keeps pupils constricted throughout the day.

The PLR relies on a subcortical, parasympathetic pathway that carries luminance information from photoreceptors in the retina, via the pretectal olivary nucleus and the Edinger-Westphal nucleus (EWN), and back toward the eye, where contraction of the iris sphincter muscle results in pupil constriction (Kardon 2005, McDougal & Gamlin 2008). The cognitive influences on the PLR that I discuss in Sections 3 and 4 likely reflect a modulation of this subcortical pathway by cortical brain areas; however, the exact mechanisms behind this modulation are still unclear.

2.2. The Pupil Near Response

When you shift focus from an object that is far away to an object that is nearby, three different eye movements occur in concert: vergence, an inward rotation of the eyes that brings the nearby object into central vision for both eyes; accommodation, an increase in lens curvature that brings the nearby object into focus; and the pupil near response (PNR), a pronounced pupil constriction (Mays & Gamlin 1995, McDougal & Gamlin 2008). Together with brightness, focal distance is the main determinant of pupil size.

The neural pathway that drives the PNR is less well-understood than that of the PLR. Cortical areas, including the frontal eye fields in the macaque brain or its homolog in the human brain, may possibly project to the EWN. From there, the pathway would be identical to that of the PLR (McDougal & Gamlin 2008).

2.3. The Psychosensory Pupil Response

There are many psychological processes that are accompanied by pupil dilation, including arousal, emotion (positive and negative), mental effort, working-memory load, and motor preparation (for a review, see Beatty 1982, Beatty & Lucero-Wagoner 2000, Goldwater 1972, Laeng & Alnaes 2019, Loewenfeld 1958). These processes are varied, yet all have in common that they are characterized by a general increase in cognitive activity, which has been dubbed the intensity dimension of thought (see Just & Carpenter 1993), and that they are accompanied by a slight dilation of the pupil. I refer to this phenomenon as the psychosensory pupil response (PPR). Other authors have used different terms, such as reflex dilation, effort-related dilation, and arousal-related dilation; all of these refer to the same phenomenon.

Several authors have argued that the PPR is a nonfunctional epiphenomenon, and that its interest for psychologists lies solely in the fact that it can be used as a reporter variable for various cognitive processes (e.g., Beatty & Lucero-Wagoner 2000). However, as I discuss in Section 6, I think it is more fruitful to view the PPR as a subtle form of sensory tuning that adapts vision to the needs of the situation.

The PPR relies on a subcortical, sympathetic pathway that projects from several brain areas that reflect arousal [notably the hypothalamus, the locus coeruleus (LC), and the superior colliculus] to the eye, where contraction of the iris dilator muscle triggers pupil dilation (Kardon 2005, McDougal & Gamlin 2008).

3. PUPIL RESPONSES AND VISUAL COGNITION

The way in which visual input is processed depends on many cognitive factors, including visual attention, visual working memory (VWM), and visual mental imagery. This is the domain of visual cognition (Cavanagh 2011). The fact that many of these same cognitive factors also affect pupil size highlights that pupil responses are an integral part of visual cognition.

3.1. Covert Attention Toward the Periphery (Attentional Breadth)

The term attentional breadth refers to how diffusely attention is spread across the visual field. A broad attentional focus encompasses much of the visual periphery and contrasts with a narrow focus of attention on central vision. (This terminology implicitly characterizes attention as a zoomlight that changes size while remaining centered on central vision, rather than as a spotlight that moves around in space. This is a simplified characterization but is useful for the present purpose.)

Central and peripheral vision differ in many ways. These differences are already apparent at the level of the retina (Curcio et al. 1987). Specifically, the distribution of cones is much denser in the fovea than in the retinal periphery; this is especially the case for red- and green-sensitive cones but is to some extent also the case for blue-sensitive cones. In contrast, rods are distributed more uniformly across the retina, with a peak density in the dorsal retina, which corresponds to the lower visual field. Given the many differences between central and peripheral vision, and assuming that pupil size adapts to the demands of the situation, the question arises whether pupil size varies as a function of whether attention is narrowly focused on central vision, or rather is diffusely spread across peripheral vision; that is, does attentional breadth affect pupil size?

To address this question, Daniels et al. (2012) presented an array of stimuli to participants. Some of these stimuli were near (but just outside of) central vision, while other stimuli were placed further into peripheral vision. Participants were instructed to shift their focus of attention between the central and the peripheral stimuli, as indicated by rhythmic changes in color of a central fixation dot. Crucially, Daniels et al. (2012) found that these rhythmic changes in attentional breadth also induced rhythmic changes in pupil size, suggesting that pupil size is affected by attentional breadth (see also Brocher et al. 2018, Mathôt & Ivanov 2019).

More recently, Ivanov et al. (2019) conducted an experiment designed to address some of the limitations of previous work. Specifically, they directly measured pupil-size changes in response to shifts of attention, rather than conducting a time-frequency analysis, as done by Daniels et al. (2012). In addition, they kept the task [unlike Mathôt & Ivanov (2019)], difficulty, and visual stimulation [unlike Brocher et al. (2018)] constant across all conditions. Participants saw patches of tilted lines (Gabor patches), three on each side of fixation, at various eccentricities (**Figure 1a**). Participants indicated the orientation of two targets, which were tilted Gabor patches, one on each

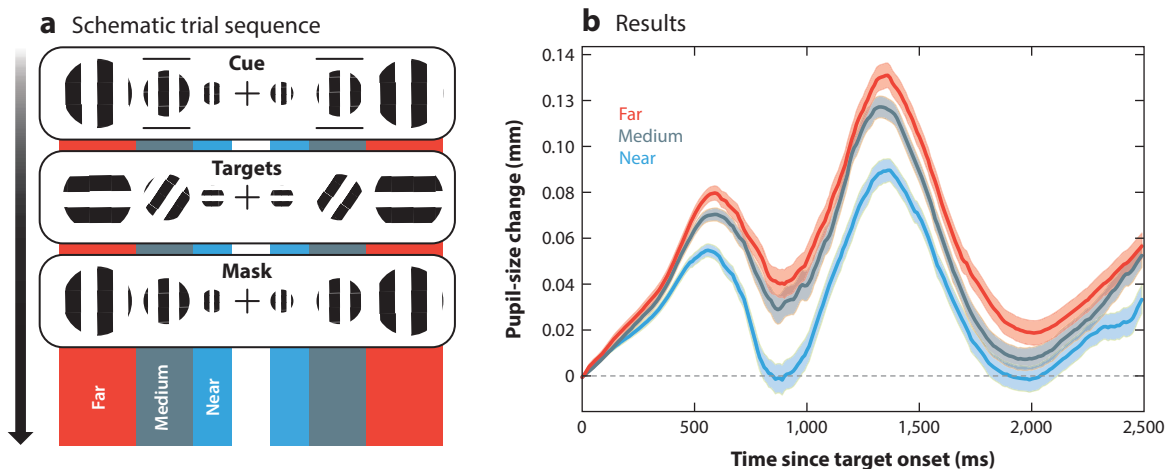


Figure 1

Schematic paradigm and results of Ivanov et al. (2019). (a) Participants discriminated a precued target stimulus that could be presented at different eccentricities (near, medium, far). (b) Pupil size after target presentation increased with increasing target eccentricity.

side of fixation. A precue indicated whether the targets would be presented at the near, medium, or far eccentricity. Crucially, Ivanov et al. found that pupil size increased with increasing eccentricity of the attended location (**Figure 1b**).

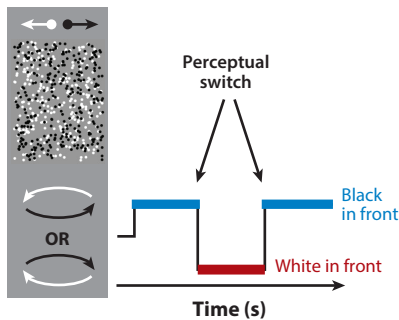
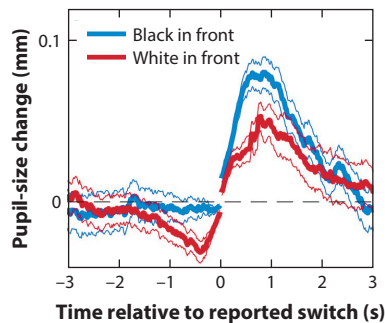
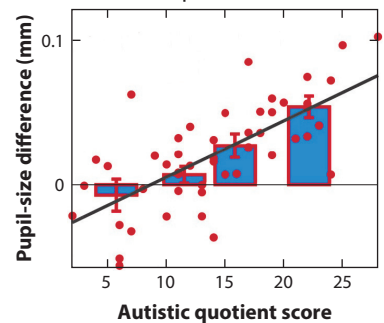
In summary, the studies by Daniels et al. (2012), Brocher et al. (2018), Ivanov et al. (2019), and Mathôt & Ivanov (2019) suggest that the size of the pupil flexibly adapts to attentional breadth; specifically, the pupil is larger when attention is diffusely spread across a large part of the visual field, as compared to when attention is narrowly and centrally focused.

3.2. Attention to, Working Memory of, and Imagery of Bright or Dark Stimuli

The PLR was traditionally considered a low-level reflex to light, and not something that is susceptible to cognitive influences. The PLR is indeed reflexive in the sense that it is a stereotyped response that is automatically triggered by light: If someone shines a light in your eye (and assuming that you are neurologically intact), your pupils will always constrict and never dilate, and this constriction will always have the same stereotyped profile as described in Section 2. However, cognitive factors can increase or decrease the strength of the PLR and even induce a (weak) PLR-like response in the absence of direct visual stimulation.

In one experiment, Mathôt et al. (2014) tested whether reflexive shifts of attention towards bright or dark objects affect pupil size (see also Binda et al. 2013, Mathôt et al. 2013, Naber et al. 2013, Unsworth & Robison 2017). Participants fixated in the center of a display that was horizontally divided into a bright and a dark half. Two patches of lines were presented, one on the bright side of the screen and one on the dark side. Next, one of these patches seemed to move for 50 ms (through a continuous phase change that induces a motion signal), which captures attention reflexively. Crucially, Mathôt et al. found that, when attention was captured toward the bright side of the screen, the pupil was smaller than when attention was captured toward the dark side. That is, even when visual input and eye position are controlled, covert spatial attention toward brightness or darkness affects pupil size.

In the study described above, attention was directed to a bright or dark location in space. However, even when bright and dark stimuli overlap in space, selectively attending to either stimulus

a Stimulus and perceptual switches**b** Pupil size as a function of perceived front color**c** Pupil-size difference (black – white) as a function of autistic quotient**Figure 2**

Schematic paradigm and results of Turi et al. (2018). (a) Participants viewed two superimposed fields of dots, one black and one white, moving in opposite directions. Subjectively, either the black (*blue line*) or white (*red line*) field is perceived as being in front, and perception frequently switches between the two. (b) When the black field is perceived as being in front, the pupil is larger than when the white field is perceived as being in front. (c) The pupil-size difference (black – white) is larger for participants who score high on autistic traits. Figure adapted from Turi et al. (2018) (CC BY-SA 4.0).

affects the size of the pupil (i.e., feature-based, as opposed to spatial, attention). In a recent study, Turi et al. (2018) presented two superimposed fields of random dots moving in opposite directions (**Figure 2a**). One field consisted of bright dots, and the other field consisted of dark dots (see also Binda et al. 2014). Perceptually, this type of stimulus gives the impression of a rotating cylinder, where the direction of rotation depends on which field is attended and which field is thus perceived as being in front. Based on the direction of rotation that participants reported, the authors could therefore determine whether participants were attending to the bright or the dark field. The authors found that feature-based attention toward brightness or darkness affects pupil size, in line with the results of similar studies on spatial attention (**Figure 2b**). Strikingly, the authors also found strong but systematic individual differences in the strength of this effect; specifically, pupil size was affected most strongly in participants who scored high on autistic traits (**Figure 2c**), presumably because these participants tend to focus more strongly on details (in this case the front surface of the cylinder) than on the whole. This finding illustrates that pupil size reflects not only basic perceptual processes, but also individual differences in visual cognition.

In the studies described above, bright or dark stimuli were always visible to the participant; therefore, changes in pupil size resulted from an interaction between visual input and cognitive processes. But are cognitive processes by themselves sufficient to elicit a PLR, even in the absence of visual stimuli? Several recent studies have shown that this is indeed possible. In a series of experiments, Husta et al. (2019) asked participants to maintain both a dark and a bright stimulus in VWM (see also Zokaei et al. 2019). After the stimuli had been removed, a retrocue indicated which of the two stimuli would be probed later. Crucially, Husta et al. found that, when the dark stimulus was cued, pupil size was larger than when the bright stimulus was cued. This shows that, even when there is no direct visual stimulation, a mental representation of brightness or darkness is sufficient to (slightly) change the size of the pupil. Other studies, which used mental imagery (Laeng & Sulutvedt 2014) or word comprehension (Mathôt et al. 2017) to elicit a mental representation of brightness or darkness, have found similar results.

In summary, the PLR is a reflex that is modulated by visual cognition. That is, a flash of light always triggers a reflexive pupil constriction, but the strength of this constriction is modulated by visual cognition. A small PLR-like response can even be elicited by a mental representation of brightness or darkness in the absence of visual stimulation.

3.3. Mental Imagery of Stimuli that Are Nearby or Far Away

To date, most studies that have looked at interactions between visual cognition and pupil size have focused on the PLR. However, there is some evidence that the PNR is affected by some of the same cognitive factors that affect the PLR. The most compelling evidence so far comes from a study by Sulutvedt et al. (2018), in which participants were shown an object that was subsequently removed from the display. Participants were then asked to imagine the object placed either nearby or far away. Crucially, the authors found that the pupils were smaller when participants imagined nearby objects than when they imagined objects that were far away, suggesting that mental imagery can trigger a weak PNR, similar to what has been found for the PLR (Laeng & Sulutvedt 2014). Future studies will need to replicate and extend this initial finding to establish more firmly whether the PNR is indeed susceptible to cognitive influences.

4. PUPIL RESPONSES AND SPATIAL EYE MOVEMENTS

Spatial eye movements shift gaze from one location to another; such eye movements contrast with nonspatial eye movements, such as accommodation, pupil responses, and torsional eye movements, which change the properties of the eye in different ways. The two best-studied types of spatial eye movements are saccadic eye movements, which shift gaze between objects, and smooth pursuit eye movements, which track moving objects (Kowler 2011). There are strong connections between pupil responses and spatial eye movements, both in terms of overlapping neural pathways (Wang & Munoz 2015) and in the sense that eye movements are often accompanied by changes in pupil size.

4.1. Pupil Constriction After Blinks and Saccadic Eye Movements

Saccadic eye movements are followed by a pronounced pupil constriction that resembles the response to a brief flash of light: The pupils start to constrict with a latency of approximately 200–250 ms after the eye movement, and it takes approximately 3 s for them to regain their original size (Knapen et al. 2016, Mathôt et al. 2015a, Zuber et al. 1966). Eye blinks trigger a very similar pupil response (Knapen et al. 2016).

It is not entirely clear what triggers these pupil responses to blinks and saccadic eye movements. Motor activity, which causes pupil dilation (Einhäuser et al. 2010), likely plays some role. However, the main driving force may be visual change, which causes a transient pupil constriction even without changes in overall luminance (Sahraie & Barbur 1997, Slooter & van Norren 1980, Ukai 1985, Van de Kraats et al. 1977). For example, when you look at a checkerboard that inverts polarity (all white tiles become black and vice versa), the pupils briefly constrict (Slooter & van Norren 1980).

Eye movements are accompanied by large shifts of visual input across the retina, and blinks are accompanied by a brief but severe blanking of visual input. The hypothesis that these visual changes are what trigger pupil constriction after blinks and eye movements is supported by the finding that, when additional visual change is introduced during an eye movement (in the form of an intrasaccadic percept), the subsequent pupil constriction also becomes more pronounced (Mathôt et al. 2015a).

4.2. Preparation of Saccadic Eye Movements Toward Bright or Dark Stimuli

As discussed in Section 2, when a light is switched on, the pupils constrict with a latency of 200–250 ms (Ellis 1981). However, in this situation, you are a passive receiver of brightness changes, which is far from typical of daily life. More commonly, you actively control brightness changes by making eye movements toward bright or dark objects, in which case the visual system can anticipate the changes in luminance before they occur, effectively reducing the latency of the PLR.

To test whether preparation plays a role in the PLR, Mathôt et al. (2015b) performed a simple experiment in which participants initially fixated at the center of a display that was bright on one side and dark on the other. Next, a cue instructed participants to make an eye movement either toward the left or toward the right. In one condition of the experiment, the display flipped as soon as the eyes were set in motion; that is, the side of the display that was initially dark became bright and vice versa. This allowed for a dissociation between the preparatory component of the PLR (driven by the presaccadic brightness) and its reactive component (driven by the postsaccadic brightness). Crucially, Mathôt et al. (2015b) found that the pupil started to respond to the presaccadic brightness almost immediately when the eyes were set in motion; this preparatory response then gradually dissipated until, after 450 ms, the pupils mostly responded to the postsaccadic brightness. This finding suggests that the PLR is not a passive response, but rather is prepared along with (or rather, as part of) saccadic eye movements (see also Ebitz et al. 2014).

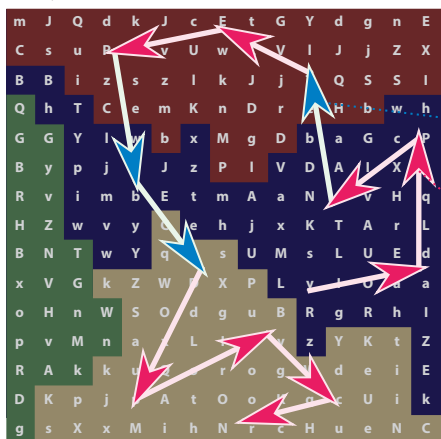
4.3. Exploration, Exploitation, and Object-Based Attention

The adaptive-gain theory (AGT) is an influential framework that links behavior to pupil size and activity in the LC, a brain-stem area (Aston-Jones & Cohen 2005). Specifically, exploration refers to a mode of behavior that is characterized by distractibility and frequent switching between tasks. Exploration would be accompanied by elevated tonic (sustained) firing of the LC but reduced phasic (event-related) firing; analogously, exploration would be accompanied by large pupils that are not very reactive to stimuli (i.e., pupil responses would reflect LC firing rates). In contrast, exploitation refers to a mode of behavior that is characterized by focus on a single task. Exploitation would be accompanied by reduced tonic and increased phasic firing of the LC and, analogously, by medium-to-small pupils that are highly reactive to stimuli. Simply put, the AGT posits that the LC is a neural control center for behavior, and that pupil size is useful as a marker of LC activity. This theory provides a useful framework, although the link between LC activity and pupil size is likely much more complex than this simplified view suggests (Joshi & Gold 2019).

Most studies of exploration and exploitation have used game-like tasks, such as the Wisconsin Card Sorting Test (Pajkossy et al. 2017) or a modified version of the Iowa Gambling task (Jepma & Nieuwenhuis 2011). In these tasks, modes of behavior are inferred from how participants play the game; for example, switching from one deck of cards to another would be indicative of exploration, whereas sticking to the same deck would be indicative of exploitation. However, the terms exploration and exploitation are also directly applicable to eye movements. In this context, exploitation would refer to within-object eye movements that inspect different parts of a person, object, or text; for example, an eye movement from “this word” to “this word” would reflect exploitation. In contrast, exploration would refer to between-object eye movements that carry gaze from one object to another; for example, an eye movement that shifts gaze away from this text to check for notifications on your smartphone would reflect exploration.

Mathôt & Regnath (2019) recently conducted an experiment to test whether the predictions of the AGT hold up in the context of eye movements in a visual-search task. In their study, participants searched for a target letter among a large number (225) of distractor letters. The search

a Search display and schematic eye movements



b Pupil size

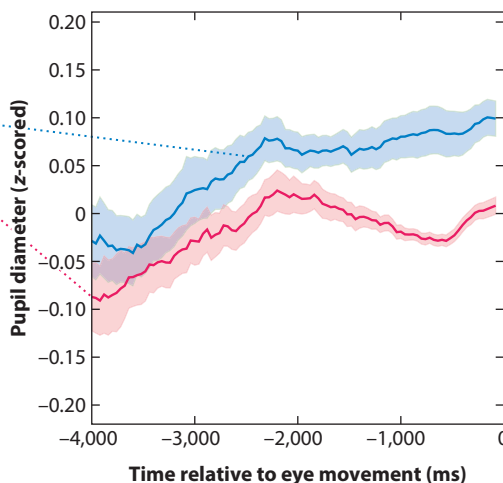


Figure 3

Schematic paradigm and results of Mathôt & Regnath (2019). (a) Participants searched for a target letter in a complex display that was randomly divided into four regions. Participants tended to first make exploitation eye movements within a region (*pink arrows*) before making exploration eye movements from one region to another (*blue arrows*). (b) The pupil was slightly larger before making exploration eye movements (*blue line*) compared to exploitation eye movements (*pink line*).

display was divided into four randomly generated regions that were defined by color (**Figure 3a**). These regions were irrelevant to the search task, but the prediction was that participants would nevertheless be sensitive to the boundaries between these regions.

Mathôt & Regnath (2019) found that participants tended to search within regions for longer than would be expected by chance; that is, participants first made exploitation-like eye movements within regions before making exploration-like eye movements that carried gaze from one region to another. Crucially, they also found that these exploration-like eye movements were preceded by a slight pupil dilation (**Figure 3b**). Although these findings are correlational (whether participants made within- or between-region eye movements was not manipulated) and should be replicated, this pattern of results is consistent with the AGT.

5. EFFECTS OF PUPIL SIZE ON VISUAL PROCESSING

Most of the research reviewed above has looked at pupil size as a function of visual input, cognitive factors, or a combination of both. However, the relationship between pupil size and visual input is bidirectional: Pupil size also affects how visual input is processed.

5.1. Effects of Pupil Size on Detection and Discrimination Performance

When considering the effect of pupil size on performance on visual tasks, it is useful to distinguish discrimination tasks from detection tasks. In a discrimination task, the goal is to identify a stimulus; a prototypical example of a discrimination task is reading. In a detection task, the goal is to detect the presence of a faint stimulus without indicating its identity; a prototypical example of a detection

task is driving through a thick fog, in which case the driver needs to respond to any kind of stimulus that might suddenly emerge from the fog.

Small pupils are generally advantageous for discrimination tasks (Campbell & Gregory 1960, Mathôt & Ivanov 2019, Woodhouse 1975). This is because the eye's lens suffers from imperfections that distort the image in various ways, for example, by blurring the image and by having a slightly different focal distance for different wavelengths of light (Liang & Williams 1997). These optical distortions become less severe with decreasing pupil size, and this leads to measurable improvements in discrimination performance. For example, human-factors research has shown that it is easier to discriminate letters when they are presented against a bright background (Buchner et al. 2009, Dobres et al. 2017, Piepenbrock et al. 2014a); this so-called positive-polarity advantage is likely due in large part to the fact that a bright background induces small pupils (Piepenbrock et al. 2014b).

Large pupils are generally advantageous for detection tasks, especially when the goal is to detect faint stimuli that are at the threshold of detectability. This is because large pupils allow more light into the eye, thus increasing the signal; that is, large pupils make it easier to distinguish something from nothing. Although surprisingly few studies have directly investigated this large-pupil advantage for detection, Mathôt & Ivanov (2019) recently found that it is easier to detect a faint stimulus presented at an unpredictable location when pupils are large, as compared to when they are small, at least when pupil size is manipulated through the brightness of the visual periphery.

The simple narrative in which large pupils benefit detection, whereas small pupils benefit discrimination, becomes more complex when considering additional factors. For example, the fact that large pupils increase the amount of light that enters the eye means that large pupils also increase the amount of retinal light scatter (Lombardo & Lombardo 2010). Retinal light scatter creates a diffuse (unfocused) veil of light across the retina, which could hinder the detection of faint stimuli. In other words, in situations where retinal light scatter is a prominent factor (for example, because there is a bright source of light somewhere, resulting in so-called discomfort glare), detection of faint stimuli might actually benefit from small, rather than large, pupils. Additional complicating factors are dark adaptation, which affects the relative extent to which vision is based on input from rods or cones and (relatedly) whether stimuli are presented in peripheral or central vision (for a review of optical factors, see Kalloniatis & Luu 1995).

In summary, small pupils improve visual acuity and are therefore generally advantageous for discrimination tasks. In contrast, large pupils improve visual sensitivity and are therefore generally advantageous for detection tasks. However, the effect of pupil size on visual performance depends on many complex interactions among the size of the pupil, the observer's goals, the state of retina, and the environment, thus allowing for many exceptions to this general rule.

5.2. Effects of Pupil Size on Brightness Perception

When the pupil dilates, more light enters the eye. Then why do you not perceive a brightening of the world whenever your pupils dilate? The primary reason is that subjective brightness perception relies strongly on indirect clues, such as context (is an object in the shadows?) and world knowledge (refrigerators tend to be white). But what if these clues are not available? Does pupil size then affect subjective brightness perception, and if so, how?

Wardhani et al. (2019) recently conducted a series of experiments to test this. In one of these experiments, participants were first instructed to remember the brightness of a reference stimulus. Next, a task-irrelevant blue or red stimulus was presented for 10 s; the shades of blue and red were equiluminant (as determined with a separate procedure before the experiment), but a prolonged blue inducer, as opposed to a red inducer, strongly activates the ipRGCs (see Section 2), resulting

in a slight sustained pupil constriction (Do 2019). Finally, a tester stimulus was presented, and participants indicated whether the tester was brighter or darker than the referent.

Wardhani et al. (2019) determined how bright the tester needed to be in order to be perceived as equally bright as the referent as a function of whether the pupil was small (blue inducer) or large (red inducer). Crucially, they found that the brightness of the tester was underestimated when the pupil was large, as compared to when it was small. In other words, even though more light enters the eye when the pupil dilates, stimuli are perceived as less bright.

One interpretation of this result is that subjective brightness perception takes into account information about pupil size, either through proprioception (information about bodily states) or through a corollary discharge (a copy of the motor commands that control pupil size, sometimes also called an efference copy) (for a review, see Sommer & Wurtz 2008). The notion that visual input is combined with proprioception or an efference copy is commonly used to explain visual stability across eye movements (see Wurtz 2008, Mathôt & Theeuwes 2011): Eye movements dramatically change how the world is projected onto the retina, yet these retinal changes are not perceived as movement, presumably in part because the visual system relies on proprioception and a corollary discharge to distinguish self-generated movement from movement in the world. A similar mechanism may allow us to distinguish self-generated changes in retinal illumination from changes in brightness in the world; specifically, an increase in retinal illumination would be discounted when accompanied by pupil dilation. Wardhani et al.'s (2019) finding that stimuli are subjectively perceived as less bright with increasing pupil size could indicate an overcompensation for the increased retinal illumination that accompanies pupil dilation.

In summary, an initial study on the relationship between subjective brightness perception and pupil size suggests that larger pupils may lead to an underestimation of brightness. However, this result should be replicated and verified with different methods to manipulate pupil size.

5.3. Effects of Pupil Size on Visuocortical Processing

Changes in pupil size dramatically affect how light enters the eye and therefore should, in some way, affect how the brain processes this information. However, exactly how pupil size affects visuocortical processing is not entirely clear.

Several studies have looked at correlations between pupil size and activity in visual cortex using functional magnetic resonance imaging (fMRI) (e.g., DiNuzzo et al. 2019, Murphy et al. 2014). Strikingly, these studies found that larger pupils are associated with decreased activity in the visual cortex. For example, Mathôt & Hanke (2019) recently looked at the correlation between pupil size and cortical activity while participants were watching a movie in an fMRI scanner. They found that activity in the visual cortex correlated negatively with pupil size. Importantly, this negative correlation appeared not to be driven by luminance, but rather by the amount of visual change in the video. That is, bright scenes lead to smaller pupils than do dark scenes but do not lead to increased visuocortical activity, presumably because the brightness of visual input is normalized at a very early level of processing (Carandini & Heeger 2012); however, scenes with lots of movement (or other kinds of visual change) lead to both smaller pupils and increased visuocortical activity. A tentative interpretation of this finding is that the strong negative correlation between pupil size and visuocortical activity does not reflect a causal link, but rather is mediated by other factors, notably the amount of change in visual input.

Thigpen et al. (2018) looked at the link between pupil size and cortical activity using a different method. They recorded pupil size and electroencephalography (EEG) while participants viewed flickering stimuli, which result in rhythmic neural activity or steady-state visual evoked potentials (ssVEPs). The power of ssVEPs is a general measure of the strength of neural processing; for

example, attended stimuli elicit stronger ssVEPs than unattended stimuli (Morgan et al. 1996). Thigpen et al. (2018) found that natural fluctuations in pupil size did not correlate with ssVEP strength, consistent with the idea that changes in retinal illumination are normalized and therefore do not affect cortical processing.

The only study to date to have looked at how pupil size causally affects cortical processing was conducted by Bombeck et al. (2016), who also used EEG. In one of their experiments, pupil size was manipulated by having participants covertly attend to a bright or a dark stimulus in the periphery while maintaining central fixation (see also Binda et al. 2013, Mathôt et al. 2013). Next, a task-irrelevant stimulus was briefly presented either in the upper or the lower visual field. The authors then looked at the C1, an event-related potential (ERP) component that is believed to reflect the very earliest stage of visual processing. Crucially, Bombeck et al. (2016) found that large pupils resulted in an attenuated C1. They interpreted this finding in terms of visual acuity: Large pupils would blur the input of the C1-eliciting stimulus, thus attenuating cortical responses. However, the C1-eliciting stimulus was presented in the visual periphery, where acuity is already poor, and the induced pupil-size changes were minute (0.2 mm in diameter in one experiment, and only 0.02 mm in diameter in another), which would result in only a very slight blurring of visual input; in other words, it is not clear whether the attenuation of the C1 could indeed have been due to their pupil-size manipulation, or whether it was inadvertently driven by some other aspect of the paradigm.

Why has a clear link between pupil size and visuocortical activity proven so elusive? Plausibly, the effects of pupil size on visual perception, and thus on visuocortical activity, are most pronounced when stimuli are near the threshold of perception. That is, small pupils enhance perception of fine detail, but this effect is only evident for stimuli that are near the threshold of discriminability, such as very small letters (Mathôt & Ivanov 2019, Piepenbrock et al. 2014a). Moreover, large pupils enhance detection of faint stimuli, but (although direct evidence for this is missing) this effect may again only be evident for stimuli that are near the threshold of detectability. This provides a clear direction for future studies, which should (*a*) directly manipulate pupil size, rather than relying on spontaneous fluctuations, and (*b*) use stimuli that are near the threshold of discriminability or detectability.

In summary, there is a strong negative correlation between pupil size and activity in the visual cortex (DiNuzzo et al. 2019, Murphy et al. 2014). However, this correlation may be driven by mediating factors, such as changes in visual input, rather than reflecting a causal link between pupil size and visuocortical activity. To date, there has not been a conclusive demonstration of such a causal link (but see Bombeck et al. 2016), although future studies, using near-threshold stimuli and effective manipulations of pupil size, may reveal this link.

6. A THEORY OF SENSORY TUNING

The main tenet of this article is that changes in pupil size reflect an adaptation of the senses to meet the demands of the current situation and the immediate future, a principle that I refer to as sensory tuning. How do the findings reviewed above fit into this general framework? Is there evidence that sensory tuning also applies to nonvisual modalities? Does a theory of sensory tuning lead to falsifiable predictions?

6.1. Pupil Responses Likely Improve the Quality of Vision

The beneficial effects of the PLR and PNR are reasonably well understood (Sections 2 and 3; see also Mathôt 2018). Large pupils allow more light to enter the eye, thus improving vision in

darkness, where visual sensitivity is limited by the available light (Mathôt & Ivanov 2019); therefore, pupils dilate in darkness. In contrast, small pupils focus light more sharply, thus improving visual acuity (Campbell & Gregory 1960, Woodhouse 1975); therefore, pupils constrict in brightness, when sensitivity is not limited by the available light.

Focusing on a nearby object places additional demands on visual acuity because depth of field decreases dramatically with focal distance; that is, if you focus on an object that is very nearby (say at 20 cm), then an object that is slightly further away (say at 25 cm) is already considerably out of focus. Small pupils increase depth of field by improving focus for all distances (Campbell 1957, Charman & Whitefoot 1977), and this is likely why near focus is accompanied by pupil constriction.

Whether cognitively driven pupil responses also improve the quality of vision is less clear; several authors have even argued that they do not, and that cognitive effects on pupil size are too small to be behaviorally relevant and must therefore be epiphenomenal (Beatty & Lucero-Wagoner 2000, Binda & Murray 2014). However, a careful consideration of how cognitive factors modulate pupil size under various circumstances suggests differently.

As reviewed in Section 3, the pupil is smaller when attention is focused centrally than when attention is spread diffusely across peripheral vision (Brocher et al. 2018, Daniels et al. 2012, Ivanov et al. 2019). This effect of attentional breadth on pupil size matches the properties of the retina: Cone density is far higher in the central retina than in the peripheral retina (Curcio et al. 1987), and visual acuity in central vision is consequently far superior to that in peripheral vision. The beneficial effect of small pupils on visual acuity is therefore most useful for central vision; for peripheral vision, where visual acuity is limited by the properties of the retina rather than by the focus of the lens, the benefit of small pupils is likely marginal.

A similar argument applies to the finding that the pupil is smaller when people engage in exploitation behavior, as compared to exploration behavior (Section 4; see also Aston-Jones & Cohen 2005, Jepma & Nieuwenhuis 2011), and that the pupil is smaller when the level of arousal is intermediate, as compared to high (Section 2; see also, e.g., Bradley et al. 2008). (Low arousal is associated with drowsiness.) Exploitation and intermediate arousal are characterized by a narrow focus on a single task and thus by a narrow, central focus of attention, whereas exploration and high arousal are characterized by distractability and thus by a broader, peripheral focus of attention. Therefore, the effect of attentional breadth on pupil size, the effect of exploration or exploitation on pupil size, and the effect of arousal on pupil size may all reflect the same basic principle: Small pupils are most advantageous for (attention to) central vision, whereas large pupils are most advantageous for (attention to) peripheral vision.

As reviewed in Section 4, the pupil constricts in preparation for an eye movement toward a bright stimulus (Ebitz et al. 2014, Mathôt et al. 2015b). In this case, the benefit may be one of timing: By preparing a pupil constriction along with an eye movement, the latency of the PLR effectively decreases by approximately 100 ms, as compared to the response to a light stimulus during passive viewing. This latency decrease may allow the visual system to adapt more rapidly to the changes in brightness that occur across eye movements, as the eyes move from dark to bright objects and back again (Mathôt & Van der Stigchel 2015).

The effects of attention toward (Section 2; see also Binda et al. 2013, Mathôt et al. 2013, Naber et al. 2013, Unsworth & Robison 2017), and VWM of (Husta et al. 2019, Zokaei et al. 2019), bright and dark stimuli may make up an indirect form of preparation and in this sense be related to the effect of eye-movement preparation. Specifically, a covert shift of attention toward a bright object is in some ways (Craighero & Rizzolatti 2005, Rizzolatti et al. 1987), though likely not all ways (Casteau & Smith 2019), similar to programming an eye movement to that object without actually executing that movement. Similarly, when you keep a stimulus in VWM, you generally do this

with the intention to interact with that stimulus; for example, you may keep a visual representation of a white shirt in VWM to search for that shirt in your closet. The exact relationships among eye-movement preparation, visual attention, and VWM are still debated (Casteau & Smith 2019, Xu 2017), but for the present purpose the key observation is that they can all be characterized as an intention to act; this may explain why these cognitive processes are all accompanied by pupil constriction when the target stimulus is bright and pupil dilation when the target stimulus is dark.

Despite the fact that many cognitive effects on pupil size can be understood as subtle forms of sensory tuning, some effects remain mysterious. For example, pupil dilation in response to increased memory load (Kahneman & Beatty 1966), listening effort (Zekveld et al. 2010), or cognitive load more generally (Just & Carpenter 1993) does not serve any obvious function. Perhaps these kinds of cognitive effects are indeed epiphenomenal, possibly resulting from overlap with other cognitive processes for which pupil dilation is functional.

To summarize, two key observations may explain many, though not all, cognitively driven pupil responses. First, an emphasis on central vision over peripheral vision results in pupil constriction, and this likely reflects the fact that central vision benefits most from the increased visual acuity provided by small pupils. Second, an intention to act with bright stimuli results in pupil constriction, which reduces the latency of the PLR when that bright stimulus is subsequently brought into view. Together, this pattern suggests that cognitively driven pupil responses improve the quality of vision in subtle ways that meet the demands of the situation; that is, cognitively driven pupil responses, like their reflexive counterparts, are a form of sensory tuning.

6.2. Sensory Tuning in the Auditory Modality

Above, I focus on vision. However, I propose that sensory tuning is a general principle of sensation and perception that also affects other sensory modalities, such as hearing.

The stapedius (or acoustic) reflex is a contraction of the muscles of the middle ear. This reflex reduces auditory sensitivity to low-pitch sounds, while leaving sensitivity to high-pitch sounds mostly intact (Borg 1968), and is triggered by loud sounds and the act of speaking (Borg & Zakrisson 1975). The stapedius reflex is a form of sensory tuning that optimizes the auditory sense depending on the situation. For example, speaking generates low-frequency vibrations that propagate through the skull and that overpower the mid-range frequencies of actual speech. By contracting the middle ear, thus filtering out low-frequency vibrations, the stapedius reflex makes it easier to hear yourself speaking (Borg & Zakrisson 1975). However, in other situations, when there are no irrelevant low-frequency sounds, the inner ear relaxes, thus allowing you to also hear low frequencies.

6.3. Predictions Based on a Theory of Sensory Tuning

There are many degrees of freedom when assigning functions to pupil responses: It is easy to come up with convincing post hoc explanations for why the pupil responds when and as it does. A stronger test of a theory of sensory tuning is to make (and test) predictions about how the pupil should respond in so-far untested situations.

A first prediction follows from the hypothesis that cognitively driven pupil dilation reflects an emphasis on peripheral vision at the expense of central vision. Central vision is severely impaired for people who suffer from macular degeneration (Ferris 1983), and most people with this condition develop a strategy where they consistently use a specific part of their peripheral vision (the so-called preferred retinal locus) as a stand-in for their impaired central vision (Fletcher & Schuchard 1997). Crucially, for people who suffer from macular degeneration, there is no

clear-cut distinction between central and peripheral vision. Consequently, I predict that people who suffer from macular degeneration should show markedly reduced cognitively driven pupil dilation in situations where people without visual impairment do show such dilation, for example, when switching from an exploitation to an exploration mode of behavior.

A second prediction follows from the finding that the pupil constricts when maintaining a bright stimulus in VWM (Husta et al. 2019, Zokaei et al. 2019) and the hypothesis that this reflects an indirect intention to act upon that stimulus. A prominent notion in the field of VWM is that VWM items can be in different states (for reviews, see Olivers et al. 2011, Wolff et al. 2017, Zokaei et al. 2014). Items that are likely to be acted upon in the immediate future are kept in a so-called active or prioritized state; the number of items that can simultaneously be in an active state may be more limited than the capacity of VWM, although the extreme view that only a single item can be active at a time (Olivers et al. 2011) is likely too restrictive (Zhou et al. 2020). In contrast to this active state, items that should be remembered but are unlikely to be acted upon in the immediate future are kept in a so-called silent or accessory state. Crucially, I predict that the brightness of VWM items should only affect pupil size when these items are in an active state. This prediction can be tested by having participants memorize bright and dark items, and by using various techniques to control the state of VWM items (for a review, see Zokaei et al. 2014).

A third prediction follows from the hypothesis that sensory tuning is a general principle that applies also to the auditory modality. As described above, the stapedius reflex reduces or increases sensitivity to low-frequency sounds depending on the situation (Borg 1968). However, it is still an open question whether the stapedius reflex is modulated by cognitive factors in the same way that the pupil light response is. [However, Jones et al. (2019) recently showed that the stapedius reflex is likely not susceptible to classical conditioning.] This could be tested in an experiment in which participants hear two simultaneous streams of sounds, one with a high pitch and one with a low pitch. Participants would attend to one of the streams. Crucially, I predict that the middle ear should contract when participants attend to the high-pitch stream, as compared to when participants attend to the low-pitch stream.

To summarize, the theory of sensory tuning that I put forward in this article leads to falsifiable predictions, three of which I outline above.

7. CONCLUSION

Sensation is often described as a passive response of receptors to external stimulation. According to this view, cognitive processes affect sensory processing only at a later, perceptual stage, when processes such as attention and prediction shape how sensory information is processed (Cavanagh 2011). The key tenet of this review is that the classic dichotomy between sensation and perception is far too restrictive, and that cognition affects sensation at every stage; our senses are active organs with substantial freedom of movement, and we continuously tune our senses to meet the demands of the current situation and the immediate future.

In this review, I focus on changes in pupil size as one specific form of sensory tuning. I review the various ways in which pupil size is affected by sensory input (Section 2), by cognitive processes (Sections 3 and 4), and by the interaction between them. I propose that cognitive processes that are characterized by an emphasis on central vision over peripheral vision are accompanied by pupil constriction (Section 6) because central vision benefits from the high visual acuity offered by small pupils, whereas peripheral vision does not, or hardly does (Section 5). In addition, cognitive processes that are characterized by an intention to interact with bright stimuli are accompanied by preparatory pupil constriction, so as to reduce the latency of the PLR when that bright stimulus is subsequently brought into view (Section 6).

Although the focus of this review is on vision, I propose that sensory tuning is a general principle that applies to all sensory modalities. As one example from the auditory modality, I discuss the stapedius (acoustic) reflex (Section 6; see also Borg 1968). The stapedius reflex is a contraction of muscles in the middle ear that results in a reduced sensitivity to low-frequency sounds. This allows the ear to be selectively sensitive to low-frequency or high-frequency sounds as the situation demands.

To summarize, our eyes are controlled by fourteen muscles that move and shape the eyes, so that we can sense light in different ways that are optimized for different situations. Pupil responses are but one fascinating example of such sensory tuning.

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Errata

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