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Research Paper

Multisensory integration in orienting behavior: Pupil size, microsaccades, and saccades

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A B S T R A C T

Signals from different sensory modalities are integrated in the brain to optimize behavior. Although multisensory integration has been demonstrated in saccadic eye movements, its influence on other orienting responses, including pupil size and microsaccades, is still poorly understood. We examined human gaze orienting responses following presentation of visual, auditory, or combined audiovisual stimuli. Transient pupil dilation and microsaccade inhibition were evoked shortly after the appearance of a salient stimulus. Audiovisual stimuli evoked larger pupil dilation, greater microsaccade inhibition, and faster saccade reaction times compared to unimodal conditions. Trials with faster saccadic reaction times were accompanied with greater pupil dilation responses. Similar modulation of pre-stimulus pupil-size-change rate was observed between stimulus-evoked saccadic and pupillary responses. Thus, multisensory integration impacts multiple components of orienting, with coordination between saccade and pupil responses, implicating the superior colliculus in coordinating these responses because of its central role in both orienting behavior and multisensory integration.

1. Introduction

Salient events in the environment initiate orienting responses including gaze shifts and pupil dilation (Boehnke & Munoz, 2008; Sokolov, 1963). Salient stimuli can be of different modalities and therefore activate more than one sense, and to detect and react optimally, the signals induced by different modality stimuli are combined and integrated in the brain (Stein & Meredith, 1993). Orienting behavior is typically enhanced towards presentation of multi-modal stimuli that are aligned in space and time compared to uni-modal stimuli, a phenomenon referred to as multisensory enhancement (e.g., Corneil, Van Wanrooij, Munoz, & Van Opstal, 2002; Stein & Stanford, 2008; Stevenson et al., 2014). While providing great insights into multisensory processing, these investigations have been mostly confined to saccadic eye movements.

Pupil dilation and microsaccade occurrence are additional components of orienting (Corneil & Munoz, 2014; Wang & Munoz, 2015). Transient pupil dilation can be evoked following the appearance of salient stimuli, and is systematically modulated by stimulus saliency, with faster and larger evoked responses for higher stimulus contrast (Wang, Boehnke, Itti, & Munoz, 2014; Wang & Munoz, 2014). Microsaccade generation is also modulated by stimulus presentation (Hafed, 2011; Martinez-Conde, Otero-Millan, & Macknik, 2013), with suppression shortly after stimulus appearance (known as microsaccade inhibition), followed with an increased rate of microsaccade occurrence (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Valsecchi & Turatto, 2009).

Components of orienting, if guided by the same underlying neural mechanisms, should be coordinated. The midbrain superior colliculus (SC) receives convergent visual, auditory, and somatosensory inputs, and is considered one of the most important structures for multisensory integration (Stein & Meredith, 1993) and coordination of the orienting response (Boehnke & Munoz, 2008; Corneil & Munoz, 2014). The central role of the SC on pupil dilation and microsaccade generation has recently been revealed through several lines of evidence. Transient pupil dilation can be evoked by weak electrical microstimulation of the SC of behaving monkeys (Wang, Boehnke, White, & Munoz, 2012) and the optic tectum of owls (Netser, Ohayon, & Gutfreund, 2010). Furthermore, the effects of stimulus contrast, modality, and saccade preparation on the pupil response (Wang et al., 2014; Wang, Brien, & Munoz, 2015; Wang & Munoz, 2014) are similar to those observed on activity recorded from single neurons in the SC (Everling, Dorris, Klein, & Munoz, 1999; Marino et al., 2012; Wise & Irvine, 1983). Finally, the SC has been implicated in the generation of microsaccades, showing movement-related neural activity prior to microsaccade onset, with each neuron spatially tuned to a certain microsaccade direction and amplitude similar to tuning observed for macrosaccades (Hafed, Goffart, & Krauzlis, 2009; Hafed & Krauzlis, 2012).

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Here we investigate how multisensory integration impacts pupillary, microsaccadic, and saccadic responses in humans following the presentation of visual, auditory, or combined audiovisual stimuli. We hypothesize that sensory signals induced by stimuli of different modalities are integrated to produce coordinated orienting responses, enabling stronger orienting responses of pupil size, microsaccades, and saccades in the audiovisual condition, compare to the visual or auditory-alone condition. Furthermore, if saccade and pupil responses are mediated by the shared circuits, then evoked saccadic and pupillary responses should be correlated. Namely, trials with faster saccades should be accompanied by faster pupil responses. Moreover, the rate of pupil size change prior to stimulus appearance (baseline epoch) is known to modulate ensuing responses (Reimer et al., 2014). Because of the overlapped neural substrates, the influence of baseline pupil size change rate should be observed not only on saccade reaction times in saccade trials but also on stimulus-evoked pupil responses in fixation trials.

2. Materials and methods

2.1. Participants

All experimental procedures were reviewed and approved by the Queen's University Human Research Ethics Board in accordance with the declaration of Helsinki. Twenty participants ranging between 18 and 35 years of age were recruited for this study. All participants had normal or corrected-to-normal vision, were naïve to the purpose of the experiment, provided informed consent, and were compensated for their participation.

2.2. Recording and apparatus

Eye position and pupil size were measured by a video-based eye tracker (Eyelink-1000 binocular-arm, SR Research, Osgoode, ON, Canada) at a rate of 500 Hz with binocular recording (left pupil was mainly used). Stimulus presentation and data acquisition were controlled by Eyelink Experiment Builder and Eyelink software. Stimuli were presented on a 17-inch LCD monitor at a screen resolution of 1280 × 1024 pixels (60 Hz refresh rate), subtending a viewing angle of 32° x 26°, and distance from the eyes to the monitor was set at 58 cm. Pupil area values recorded from the eye tracker were transformed to actual pupil size in diameter following previously described methods (Steiner & Barry, 2011; Wang et al., 2012; Wang & Munoz, 2014). Pupil size data can be distorted by eye movements because the size of the pupil depends on the angle of the eyeball in a video-based eye tracker. Saccade generation could also confound our test of the role of stimulus contrast on the evoked pupil responses, because any observed differences in pupil response between different conditions could be triggered by saccadic eye movement itself, rather than stimulus contrast per se. To maintain an accurate measure of pupil size before, during, and after visual stimulation and to avoid contamination by saccadic eye movements, participants were required to maintain visual fixation on a point at the center of the screen throughout the trial except for the trials that required saccadic eye movements.

2.3. Behavioral task (Fig. 1A)

Participants were seated in a dark room (background noise ~40 dB) and the experiment consisted of 210 trials. Each trial began with the appearance of a central fixation point (FP) (0.6° diameter; 6 cd/m^2) and two black open circle placeholders (0.6° diameter; 12° eccentricity to the left and right of FP on the horizontal axis) on a gray background (11 cd/m^2). After 1–1.4 s of central fixation, a peripheral stimulus was presented for 100 ms to the left or right of the FP (~12° eccentricity on the horizontal axis) on a subset of trials (90 trials) and participants were required to maintain steady fixation for an additional 2–2.5 s (Fix condition, Fig. 1A). Three types of peripheral stimuli were used, namely, visual (black, 0.6° diameter), auditory (60 dB SPL, narrow-band noise ranging from 2000 to 4000 Hz generated by Matlab software), or audiovisual (combined visual and auditory stimuli). There was also a no stimulus control (Ctrl condition, Fig. 1A) condition on a subset of trials (30 trials). In addition, to examine the effects of multisensory integration on saccadic behaviors and to also prevent the participant from strategically ignoring the peripheral stimulus, on another proportion of trials (90 trials), the FP was removed simultaneously with stimulus appearance (100 ms), and the participant was required to generate a saccade toward the stimulus (Sac condition, Fig. 1A), and maintain fixation until the disappearance of placeholders (1000 ms). Stimulus location (left and right), stimulus type (visual, auditory, and audiovisual), and task condition (Fix, Ctrl, and Sac) were randomly interleaved.

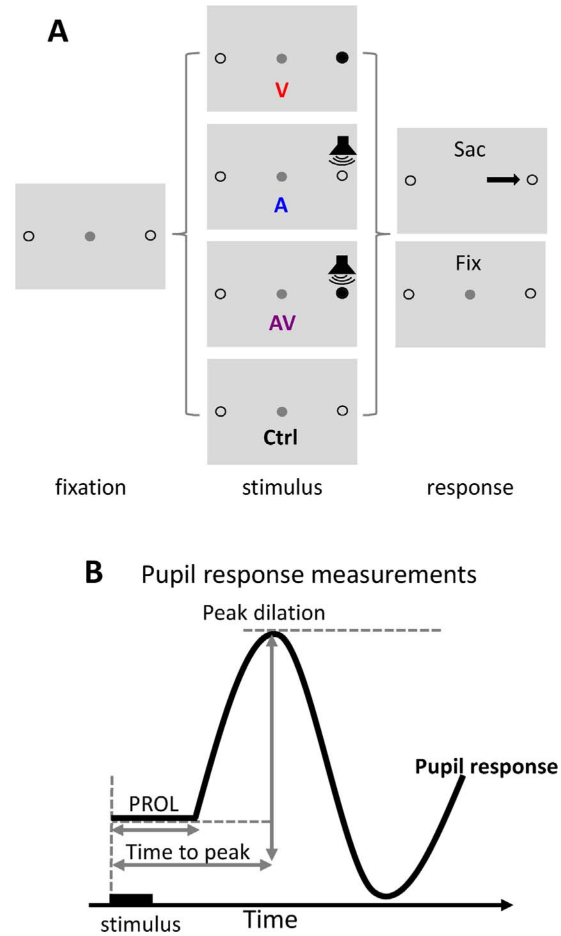

Fig. 1. A) Each trial started with a central fixation point on a gray background. After a random delay there was a brief presentation (100 ms) of a visual, auditory, or audiovisual stimulus (Fix) or no stimulus presented (Ctrl) and participants required to maintain central fixation for another 2-2.5 s. In some trials, the presentation of visual stimuli coincided with the disappearance of central fixation, and participants required to move their eyes to the stimulus (Sac). **B)** Measurements of the evoked pupil response. PROL: pupil response onset latency, V: visual, A: auditory, AV: audiovisual, Ctrl: control (no stimulus).

The current study used relatively low intensity for auditory stimuli to induce multisensory integration because multisensory integration is stronger using lower stimulus contrast (Fetsch, DeAngelis, & Angelaki, 2013; Populin & Yin, 2002; Stanford, Quessy, & Stein, 2005). Note that the sounds were presented from small speakers attached to the middle position of the left or right side of the monitor, and therefore there was a subtle difference on the horizontal location between visual and auditory stimulus (~3°). To reduce this potential influence, as mentioned, there were two placeholders on the left and right of the FP, and