Luminance and contrast in visual perception of time to collision

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ABSTRACT

Many animals avoid dark, approaching objects seen against a lighter background but show no or weaker reactions to stimuli with inverted contrast. We investigated whether human observers would respond differently to such stimuli in terms of estimated time-to-arrival. We varied luminances of an approaching, light or dark disk and a plain, grey background, and for several conditions, continuously adjusted calibrations so as to keep contrast and/or overall lightness constant. Since no effects were found, we conclude that humans are able to discard luminance and contrast for the task at hand. Generally, however, performance was affected by different, consecutive regimes of feedback: Initially, without feedback, observers responded inconsistently and much too late; they improved after correct feedback, and in a third block of trials with pseudo-random feedback, they responded increasingly early without reverting to the initial level of uncertainty. We discuss our findings with regard to implications for neural mechanisms, put them in the context of evolutionary considerations, and propose continuative animal behavioral studies.

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1. Introduction

In vision, *looming* refers to geometrical–optical, trigonometric magnification of a surface or surface patch during approach (Gibson, 1958). Avoidance responses to such stimuli have been observed in many animal species including humans of all ages (Ball & Tronick, 1971; Bower, Broughton, & Moore, 1970; Carlile, Peters, & Evans, 2006; Dunkeld & Bower, 1980; Hayes & Saiff, 1967; King et al., 1992; Schiff, Caviness, & Gibson, 1962; Tammero & Dickinson, 2002; Yamawaki, 2011). While some animals seem to respond at certain threshold values of the increasing visual angle (Robertson & Johnson, 1993; Schiff, 1965; Yamamoto, Nakata, & Nakagawa, 2003), others appear able to take approach velocity into account and compute time-to-collision (t_C) (Sun, Carey, & Goodale, 1992; Wang & Frost, 1992). Neural mechanisms mediating these responses have been described in some detail for several species, including crab (Oliva, Medan, & Tomsic, 2007), locust (Gabbiani et al., 2002; Gray, Blincow, & Robertson, 2010; Hatsopoulos, Gabbiani, & Laurent, 1995; Jones & Gabbiani, 2010; Rind, 1996, 1997; Rind & Simmons, 1992, 1999), goldfish (Preuss et al., 2006), frog (Ishikane et al., 2005), and pigeon (Frost & Sun, 1997, 2004; Sun & Frost, 1998; Wu et al., 2005; Xiao & Frost, 2009; Xiao, Li, & Wang, 2006). Importantly, some of these studies not only demonstrate looming or t_C sensitivity in the visual system but also a tight correlation (Wang & Frost, 1992) or even causal nexus (Preuss et al., 2006) with subsequent motor behavior. Less information is

available for mammals, especially humans (Billington et al., 2010; Field & Wann, 2005; Graziano & Cooke, 2006; Liu, Wang, & Li, 2011; van der Weel & van der Meer, 2009).

Many animals respond only to a dark looming object seen against a lighter background, for example, crabs (*Uca pugnax*), frogs (*Rana pipiens*), and domestic Kimber chicks (Schiff, 1965), while others show weaker responses to contrast-inverted stimuli, for example, another species of crab (*Chasmagnathus granulatus*) (Oliva, Medan, & Tomsic, 2007) and locusts (Rind & Simmons, 1992). Again, matters are less clear for mammals. Recently, Münch et al. (2009) discovered approach-sensitive retinal ganglion cells in transgenic mice. These cells could be classified as OFF-type, that is, they were excited by light decrements and inhibited by light increments (Schiller, 1992, 1995; Westheimer, 2007). The cells responded to overall dimming, and also to rapid, 1.5–11.5 deg s^{-1} magnification of a dark bar, even during concomitant overall brightening of the visual field (with total light intensity remaining constant). The effective stimulus then, besides dimming, was near-symmetric expansion of a negative-contrast boundary. Münch et al. (2009) have not yet found corresponding ON-type cells (i.e., cells that are excited by light increments and inhibited by light decrements). Although the mouse may not always be the most appropriate model organism for humans (Huberman & Niell, 2011; Hughes, 1977; Van Hooser & Nelson, 2006; Vaughan et al., 2006), the similarities observed in the anatomy and functioning of eyes across different species or even taxa make derivation of hypotheses about vision mechanisms in humans, based on what is seen in other animals, not altogether unreasonable (Franz, 1934; Joselevitch & Kamermans, 2009; Lamb, Arendt, & Collin, 2009; Schiviz et al., 2008; Walls, 1942).

We conducted two psychophysical experiments to test the conjecture that responses to looming by humans – like in most animals studied so far – are mainly driven by OFF-mechanisms (dark objects seen against a light background, or general light decrement) rather than ON-mechanisms (light objects seen against a dark background, or general light increment). Some previous work might suggest otherwise. Regan and Beverley (1978), acting as their own subjects, observed specific threshold elevations after adapting to a small, 0.5 deg visual angle, sinusoidally oscillating square, independently of sign of lightness contrast. Regan and Beverley's stimulus, however, may not compare well with looming that fills one's visual field, as conceived by Gibson (1958). Indeed, Beverley and Regan's (1979) finding that postadaptation thresholds remained unaffected by rectangles wider than 1.5 deg suggests that a different mechanism was tapped than the one responsible for the observed avoidance responses mentioned earlier (Simpson, 1988). On the other hand, Rind and Simmons (1992) and Oliva, Medan, and Tomsic's (2007) findings of weak responses to ON-stimuli in locust and crab may not generalize to mammals – humans in particular.

For our experiments we modeled achromatic looming stimuli after those of Münch et al. (2009). We expected negative-contrast stimuli to yield more precise t_C judgments than positive-contrast stimuli, irrespective of amount of contrast and overall lightness. In our general discussion, we will put our work in the context of evolution theory and ethological research.

2. Materials and methods

2.1. Participants

Two independent samples of 12 and 15 psychology undergraduates, respectively, participated in two experiments in partial fulfillment of a course requirement. In Experiment 1 there were 5 males and 7 females aged 22–36 years ($M = 25.9$, $SD = 4.25$), in Experiment 2 there were 6 males and 9 females aged 19 to 53 years ($M = 25.8$, $SD = 8.82$). Visual acuity and contrast sensitivity of observers were tested with a modified Landoldt display.

2.2. Stimuli and responses

Stimuli simulated head-on approach of an achromatic circular disk seen against a grey background. Screen size was 68 deg horizontal $\times$ 43 deg vertical visual angle. A chinrest stabilized head position. Viewing was "biocular" in the sense of Regan and Beverley (1978), that is, observers looked with both eyes but the simulation did not provide stereoscopic information. The disk was stationary for 2 s, then moved for 1–3 s at a fixed, constant speed of 4 m s^{-1}, and eventually vanished 1.5, 2, or 2.5 s prior to virtual collision. Observers were requested to press a button when they thought collision would have occurred (Carel, 1961; Schiff, 1986).

In order to prevent stereotyped responding, disk size and traveling distance were varied, yielding optical magnification of the disk from a minimum plane visual angle of 0.37–0.8 deg up to a maximum of 4–6.7 deg, with intermediate ranges in between. The first set of values closely matched those used by Regan and Beverley (1978) and Beverley and Regan (1979), the second one approximated those used by Münch et al. (2009).

2.3. Design and procedure

In order to reduce intraindividual variability and to test for effects of learning, experimental trials were initially blocked according to 3 different regimes of feedback. To obtain a baseline of performance, subjects received no feedback during the first block

of trials. Proper feedback was provided during the second block. A short green bar was shown, and the word "perfect" popped up, when responses were correct within a tolerance of ±250 ms of the true time of the disk's arrival. The bar was extended to the left for early responses (-250 ms > t_R > -500 ms) and to the right for late ones ($+250$ ms < t_R < $+500$ ms). In both cases, the bar's color turned red, and the words "too early" or "too late", respectively, appeared. For responses more than ±500 ms off the mark, the bar's color turned purple, and the words "much too early" or "much too late" appeared. During the third block of trials, feedback was pseudo-randomly assigned with the feedback "perfect" having a 60% probability to appear, and the other four possible feedbacks a 10% probability each. The purpose of this improper feedback was to test for the robustness of the reinforced responses from the second block of trials.

Experiments comprised four stimulus variants (details to be described below), two disk sizes, three presentation times, three extrapolation times, and three conditions of feedback, altogether making for 216 trials, each of which was repeated twice. Order of trials was random within the four blocks of stimulus types. Those blocks were presented in a randomized order within the three blocks of feedback conditions. Twelve practice trials with our four kinds of stimuli, but partly different parameters, were run before each experiment. Two short breaks were taken after one and two thirds of experimental trials (i.e., between the different feedback blocks). A complete session, comprising tests, practice, and experiment, lasted about 45–60 min.

3. Experiment 1

3.1. Stimuli

There are several possibilities to construct looming stimuli of constant contrast and constant overall lightness. In Table 1, we list those that we used. For Experiment 1, we only varied lightness of the looming object. In one condition, a black or white disk during motion gradually assimilated to the grey background, keeping overall lightness constant. This stimulus corresponds to a real-world scenario across the course of which an approaching object or animal (say, a predator) undergoes a change of surface reflectance, as might happen through local increases of illumination or cast shadows. Optically, this is a complex stimulus because, along with the brightening or darkening of the object there is a change (in our case, a reduction) of contrast between object and background. In a second condition, black and white disks of constant lightness were used. These stimuli, while keeping contrast constant, imply a decrease or increase of overall lightness, respectively.

3.2. Results

Data were analyzed in terms of signed errors (time of subjects' responding [t_R] minus objective t_C). As is evident from the plots in

Table 1
Overview of stimuli used in Experiments 1 (upper panel) and 2 (lower panel).

Object	Background	Contrast	Overall lightness
Black	Grey	Constant	Darkening
White	Grey	Constant	Brightening
Black, brightening	Grey	Decreasing	Constant
White, darkening	Grey	Decreasing	Constant
Black	Grey, brightening	Increasing	Constant
White	Grey, darkening	Increasing	Constant
Black, brightening	Grey, brightening	Constant	Constant
White, darkening	Grey, darkening	Constant	Constant

Note. Constant overall lightness was 21 cd m^{-2}.