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### Individual differences in context-dependent effects reveal common mechanisms underlying the direction aftereffect and direction repulsion

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#### ABSTRACT

Both spatial and temporal context influence our perception of visual stimuli. For instance, both nearby moving stimuli and recently viewed motion can lead to biases in the perceived direction of a moving stimulus. Due to similarities in the spatial tuning properties of these spatial and temporal contextdependent effects, it is often assumed that they share a functional goal in motion processing and arise from common neural mechanisms. However, the psychophysical evidence concerning this assumption is inconsistent. Here we used an individual differences approach to examine the relationship between different effects of contextual modulation on perception. We reasoned that if measures of contextual modulation share a common underlying mechanism, they should exhibit a strong positive correlation across participants. To test this hypothesis, estimates of the direction aftereffect, direction repulsion, the tilt aftereffect and contrast adaptation were obtained from 54 healthy participants. Our results show pronounced interindividual differences in the effect sizes of all four tasks. Furthermore, there was a strong positive correlation between the estimates of the direction aftereffect and direction repulsion. This correlation was also evident in the threshold elevations that accompanied these repulsive biases in perceived direction. While the effects of contrast adaptation did not correlate with any of the other tasks, there was a weak, but non-significant, correlation between the direction and tilt aftereffects. These results provide evidence for common mechanisms underlying the direction aftereffect and direction repulsion.

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#### 1. Introduction

Our perception of sensory stimuli is strongly affected by the context in which they are presented. In vision, for example, contextual modulation appears to be an ubiquitous property of processing, with psychophysical evidence for context-dependent effects across a wide range of visual attributes including orientation (Blakemore, Carpenter, & Georgeson, 1970; Gibson, 1937; Regan & Beverley, 1985), motion (Hol & Treue, 2001; Levinson & Sekuler, 1976; Marshak & Sekuler, 1979), contrast (Blakemore & Campbell, 1969; Cannon & Fullenkamp, 1991; Snowden & Hammett, 1998) and size (Blakemore & Sutton, 1969; Massaro & Anderson, 1971). These visual attributes are subject to modulation both from what surrounds the stimulus of interest (spatial context) and what has been observed in the recent past (temporal context). For instance, in motion perception, the perceived direction of a moving stimulus can be biased either by the

http://dx.doi.org/10.1016/j.visres.2016.08.009 0042-6989/© 2016 Elsevier Ltd. All rights reserved. presence of nearby moving stimuli (e.g. direction repulsion) or by recently viewed motion (e.g. direction and motion aftereffects).

Traditionally, the effects of spatial and temporal context on perception have been studied in isolation. More recently, however, a number of similarities between the characteristics of spatial and temporal contextual modulation have led some researchers to suggest that they share functional commonalities (e.g. Clifford, Wenderoth, & Spehar, 2000; Curran, Clifford, & Benton, 2006; Schwartz, Hsu, & Dayan, 2007). For example, prolonged exposure to a unidirectional motion stimulus leads to a shift in the perceived direction of a subsequent stimulus away from the adapting direction - the aforementioned direction aftereffect (Levinson & Sekuler, 1976). A similar repulsive shift in perceived direction of motion is observed if the "inducing" motion is presented simultaneously with the test stimulus (i.e. direction repulsion), either in a centre-surround configuration (Kim & Wilson, 1997; Wiese & Wenderoth, 2010) or in a transparent motion display (Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007). Furthermore, both the direction aftereffect and the direction repulsion effect demonstrate a marked similarity in their dependence on the relative directions

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of the inducer and test stimuli, with both phenomena showing the largest effects when the difference in direction between the inducer and test stimuli is between 20° and 40° (Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; Mather & Moulden, 1980; McGovern, Roach, & Webb, 2014; Schrater & Simoncelli, 1998). This similarity in the angular dependence of repulsive biases induced by spatial and temporal context has also been noted in orientation processing (Blakemore et al., 1970; Clifford et al., 2000; Schwartz et al., 2007).

While these tuning similarities are consistent with the notion that spatial and temporal contextual effects share similar neural mechanisms, such evidence is not dispositive. Indeed, there is considerable debate as to the neural substrates of the direction aftereffect (DAE) and direction repulsion (DR). For instance, while some research has provided support for the view that DR may be the result of local motion processing at an early cortical stage of the visual pathway (Grunewald, 2004; Wiese & Wenderoth, 2007, 2010), others have provided evidence favouring a global motion processing account of DR, suggesting area MT as a possible neural locus (Benton & Curran, 2003; Curran, Clifford, & Benton, 2009; Wilson & Kim, 1994). Similarly, there is conflicting evidence as to the neural origins of the DAE, with some studies providing support for a local motion processing account of the phenomena (Curran et al., 2006, 2009), while other data suggests that it arises through adaptation to global motion mechanisms residing in MT or beyond (Schrater & Simoncelli, 1998; Wiese & Wenderoth, 2007, 2010). Given that both the DAE and DR appear to exhibit characteristics of local and global motion processing, more recent accounts of these phenomena have suggested that both effects arise via multilevel processing, incorporating both early and late stages of motion analysis (Farrell-Whelan, Wenderoth, & Brooks, 2012; Wiese & Wenderoth, 2010), or through iterative processing in the same neural populations (Curran et al., 2009). However, it remains unclear whether there is any overlap in the neural representations of these two effects or whether they share a common functional

Here we take an individual differences approach to examine the relationship between the DAE and DR. We measured the DAE and DR in a large sample of participants and exploited the considerable interindividual variability inherent in the magnitude of these effects to assess whether and to what extent these measures of contextual modulation are related. This approach provided us with a powerful test of whether the DAE and DR reflect common mechanisms, as this hypothesis predicts a strong positive correlation between performance on these two measures (for an analogous approach to test for shared dimensions in the coding of face identity and expression, see Rhodes et al., 2015). Since the encoding of orientation is seen as a precursor to the encoding of direction in many models of motion processing (e.g. Simoncelli & Heeger, 1998), we also included a measure of the tilt aftereffect (TAE), a contextual effect of orientation that closely parallels the DAE (e.g. Clifford, 2002), to see whether measures on a related stimulus attribute would be correlated with the motion results. Finally, we included a measure of contrast adaptation in our test battery. Given that the encoding of contrast is very different from that of direction or orientation, we did not expect to see a correlation between the measure of contrast adaptation and any of the other context-dependent effects, however, we included this measure to test for the possibility that the size of all visual contextdependent effects are governed by a common mechanism. As well as measuring the shifts in perception induced by spatial and temporal context, we also estimated the cost in accuracy in discriminating stimuli, which is known to accompany context-dependent shifts in perception (e.g. Hol & Treue, 2001; McGovern, Roach, & Webb, 2012; Regan & Beverley, 1985) and examined whether these threshold elevations were correlated across tasks.

#### 2. Methods

#### 2.1. Participants

Fifty-four participants took part in the study. Of this fifty-four, two were excluded as reliable measurements could not be obtained on two or more of the tasks. A further three participants were excluded due to experimenter error, leaving a final sample size of forty-nine participants (mean age = 22.2, 18 male). All participants were naive to the purposes of the study, gave written informed consent prior to their inclusion and reported normal or corrected-to-normal vision. All recruitment and experimental procedures were approved by the School of Psychology Research Ethics Committee, Trinity College Dublin and the study was conducted in accordance with the principles of the Declaration of Helsinki.

#### 2.2. Stimuli and apparatus

Depending on the task, stimuli consisted of either a random dot kinematogram (RDK) or a Gabor patch. RDK patterns consisted of 350 dots presented within a circular aperture (subtending a visual angle of 6° in diameter) on a background of uniform luminance. Dot diameter and density were 0.1° and 10/deg<sup>2</sup>, respectively. On the first frame of motion, dots were randomly positioned in the circular window and thereafter displaced at a speed of 5°/s. Dots that moved outside the circular aperture wrapped around to the opposite side of the window. Gabor patches consisted of a sinusoidal grating (spatial frequency =  $1 c/\circ$ , full contrast unless otherwise stated) presented on a background of uniform luminance, windowed by a two-dimensional Gaussian envelope with a standard deviation of 1° (such that the stimulus diameter subtended a visual angle of 6 degrees at the point where it fell below 1%). All stimuli were presented on a gamma-corrected BenQ XL2410T monitor at a resolution of 1280 × 1024 pixels and refresh rate of 120 Hz. Stimuli were programmed in Python using functions from PsychoPy (Peirce, 2007, 2009).

#### 2.3. General procedure

Each participant was required to perform four different psychophysical tasks that involved either temporal or spatial contextual modulation (see Fig. 1). For each task, a baseline measure of performance (no contextual modulation) was obtained before the test measurement. For all tasks, participants were required to fixate a cross at the centre of a screen and their heads were stabilised in a chin-rest positioned 57 cm from the monitor. No feedback was presented in any of the tasks. To minimise crossover adaptation effects, tasks were performed in a fixed order for all participants designed during piloting and breaks were enforced at specific points during the test session.

#### 2.4. Tasks

#### 2.4.1. Direction aftereffect (DAE)

Participants were required to judge whether a unidirectional field of dots moved clockwise or counter-clockwise from upwards. For each trial, the direction of the stimulus on a given trial was chosen at random via the Method of Constant Stimuli. Baseline direction discrimination thresholds and points of subjective equality were measured for each participant, as well as the changes in these estimates associated with adaption to a unidirectional dot motion pattern fixed at 30° clockwise from upwards (see Fig. 1a for schematic). For baseline measurements, participants completed 2–3 runs, each consisting of 10 repeats of 9 evenly-spaced direction

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