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

David P. McGovern [a,*], Kevin S. Walsh [a], Jason Bell [b], Fiona N. Newell [a]

[a] Trinity College Institute of Neuroscience and School of Psychology, Trinity College Dublin, College Green, Dublin 2, Ireland
[b] School of Psychology, University of Western Australia, Crawley, Australia

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 context-dependent 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

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

* Corresponding author.
  E-mail address: mcgoved1@tcd.ie (D.P. McGovern).

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 multi-level 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 goal.

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 context-dependent 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^2, 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/°, 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
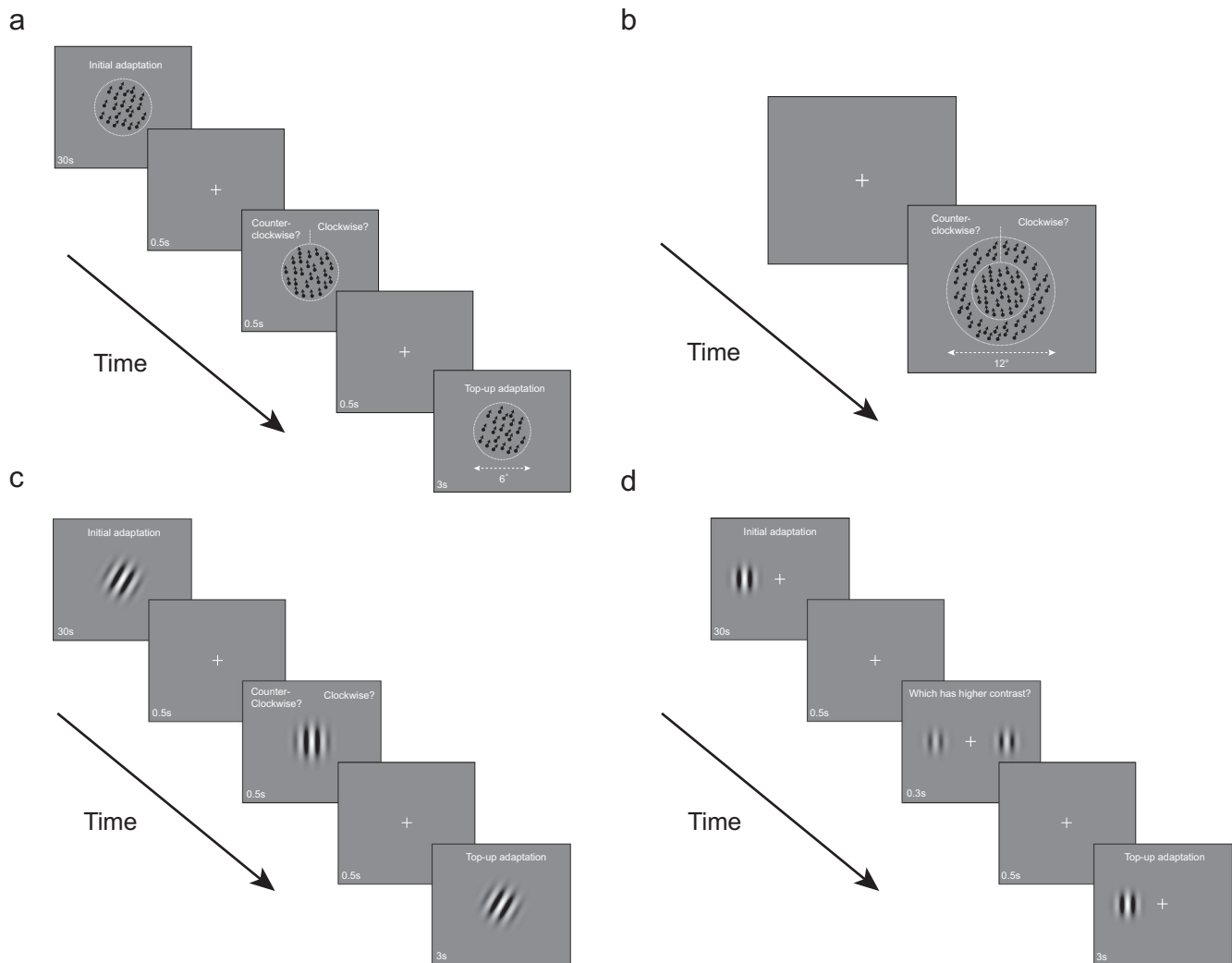
a

b

c

d

Fig. 1. Schematic illustration of the four tasks. (a) Participants judged whether a unidirectional dot motion pattern moved clockwise or counter-clockwise from upwards following adaptation to dot motion fixed at 30° clockwise from upwards. (b) Participants judged whether a unidirectional dot pattern moved clockwise or counter-clockwise, while the target stimulus was surrounded by dots moving 30° clockwise from upwards. (c) Participants judged whether a Gabor patch was tilted clockwise or counter-clockwise from vertical following adaptation to a counter-phase flickering Gabor patch oriented 30° clockwise with respect to vertical. (d) Participants judged which of two Gabor patches had the higher contrast following adaptation to a high contrast Gabor patch presented on one side of the visual field.

steps (90 trials per run) ranging between 2° clockwise to 2° counter-clockwise from upwards (step size = 0.5°). For DAE measurements, participants completed 1–2 runs of 90 trials. While the step size was fixed at 0.5°, the entire range of directions could be offset by a fixed amount depending on the participant in order to capture the full psychometric function. Pilot sessions helped to determine that a range shift of 8° could accommodate the majority of participants. If this range shift did not allow for the full capture of the psychometric function, the range shift was changed and the measurement was repeated at the end of the testing session. The initial adaptation period lasted for 30 s, with 3 s "top-ups" at the beginning of each trial thereafter. Test stimuli were presented for 0.5 s and were separated from the adapting stimulus by 0.5 s interval of mean luminance containing a fixation cross.

2.4.2. Direction repulsion (DR)

As in the direction aftereffect task, participants were required to judge whether a unidirectional dot field moved clockwise or counter-clockwise from upwards. However, in this task, the test stimulus was surrounded by dots moving 30° clockwise from upwards (see Fig. 1b for schematic). The surrounding annulus

was 12° in diameter and had the same dot density as the test stimulus. Participants completed 2 runs, each consisting of 10 repeats of 9 evenly-spaced direction steps (90 trials per run) with the direction on each trial chosen at random via the Method of Constant Stimuli. While the step size was fixed at 0.5°, the entire range of directions could be offset by a fixed amount depending on the participant in order to capture the full psychometric function. Pilot sessions helped to determine that a range shift of 8° could accommodate the majority of participants. If this range shift did not allow for the full capture of the psychometric function, the range shift was changed and the measurement was repeated at the end of the testing session. Test stimuli were presented for 0.5 s, with a 0.5 s intertrial interval.

2.4.3. Tilt aftereffect (TAE)

Participants were required to judge whether a Gabor patch was tilted clockwise or counter-clockwise with respect to vertical. For each trial, the tilt of the Gabor patch was chosen at random via the Method of Constant Stimuli. Baseline orientation discrimination thresholds and points of subjective equality were measured for each participant, as well as the changes in these estimates asso-

ciated with adaption to a counterphase flickering Gabor patch with a fixed 30° tilt from upwards (see Fig. 1c for schematic). For baseline measurements, participants completed 2–3 runs consisting of 10 repeats of 9 evenly-spaced orientation steps (90 trials per run) ranging between 1° clockwise to 1° counter-clockwise with respect to vertical (step size = 0.25°). For TAE measurements, participants completed 1–2 runs of 90 trials. While the step size was fixed at 0.25°, the entire range of orientations could be offset by a fixed amount depending on the participant in order to capture the full psychometric function. Pilot sessions helped to determine that a range shift of 2° could accommodate the majority of participants. If this range shift did not allow for the full capture of the psychometric function, the range shift was changed and the measurement was repeated at the end of the testing session. The initial adaptation period lasted for 30 s, with 3 s "top-ups" at the beginning of each trial thereafter. Test stimuli were presented for 0.5 s and were separated from the adapting stimulus by 0.5 s interval of mean luminance containing a fixation cross.

2.4.4. Contrast adaptation

Participants were required to perform a contrast-matching task (e.g. McGovern & Peirce, 2010; Snowden & Hammett, 1992), in which they judged which of two Gabor patches had the higher contrast. Unlike direction and orientation, contrast is not a circular variable such that it does not have an implicit reference (e.g. upwards) to facilitate discrimination judgments. To circumvent this problem, participants were presented with a reference Gabor patch with a fixed Michelson contrast of 30% and a test Gabor patch whose contrast varied according to a 1-up, 1-down staircase. The two Gabor patches were presented simultaneously, positioned 5° either side of a centrally presented fixation cross. Note that while this stimulus arrangement may lead to a general increase in the magnitude of the contrast adaptation effect due to stimuli being presented in the periphery (e.g. Gheorghiu, Kingdom, Bell, & Gurnsey, 2011), it should not affect the degree of interindividual variability associated with this measure or the correlations with the other tasks included in the study.

We measured the baseline point of subjective equality and change in this estimate associated with adaptation to a full contrast, counterphase flickering Gabor patch presented in the same location as the test patch (see Fig. 1d for schematic). For baseline measurements, participants completed 2 runs of 50 trials with the reference on the left and on the right (4 runs in total). For contrast adaptation measurements, participants completed a single run of 50 trials with the adaptor on the left and on the right (2 runs in total). For both the baseline and adaptation measurements, the reported PSE is the average PSE calculated across the left and right adaptor conditions. The adaptation period lasted for 30 s on the first trial, with 3 s "top-ups" at the beginning of each trial thereafter. Test stimuli were presented for 0.3 s and were separated from the adapting stimulus by 0.5 s interval of mean luminance.

2.5. Data analysis

For tasks that used the Method of Constant Stimuli, data were expressed as the proportion of trials in which a participant judged the test stimulus to be clockwise from upwards/vertical. These data points were fitted with a logistic of the form:

$$P(clockwise) = \frac{1}{\left(1 + e^{\frac{PSE-X}{JND}}\right)} \qquad (1)$$

where the point of subjective equality (PSE) is the stimulus level that leads to equal proportions of clockwise and counter-clockwise responses. The JND is an estimate of the participant's threshold for discriminating the direction/orientation of the stimu-

lus. The magnitude of the biases in perceived direction/orientation were calculated by subtracting the PSE estimate for baseline measurements from the PSE derived from conditions involving contextual modulation. Threshold elevations were calculated by dividing the JND derived from the test condition by the baseline measurement. For the contrast-matching task, the PSE was calculated as the average of the last four staircase reversals.

Following the initial fitting of the psychometric functions, two further steps were taken to prevent the inclusion of noisy data points in the correlation analysis. First, we examined goodness-of-fit statistics of each logistic fit and removed any data in which the R^2 value was less than 0.7. This step led to the removal of one data point from the direction aftereffect and two from the direction repulsion effect. Second, from the remaining data we removed any data points in which either the estimated PSE or JND was 3 standard deviations from the group mean performance on a given task. This lead to the removal of two further data points from both the direction aftereffect and direction repulsion and one data point from the contrast adaptation task. Data points were removed from a correlation if a participant's data was deemed to be an outlier or produced a poor fit on either of the tasks included in the correlation. However, this did not preclude the remaining data from a participant being included in the other correlations. Following outlier removal, we performed D'Agostino-Pearson tests on the data from each of the tasks, which indicated that all data were normally distributed. Finally, Pearson correlation was used to measure the relationship in performance between the different tasks.

3. Results

3.1. Relationship between the direction aftereffect and direction repulsion

To test whether there was a relationship between the effects of spatial and temporal context on motion perception, we measured baseline PSEs and JNDs, as well the changes to these estimates associated with contextual modulation, in a large group of participants. We reasoned that if these effects shared a common underlying mechanism, they should exhibit a strong positive correlation across individuals. The effects of spatial context on motion perception are plotted against the effects of temporal context for all participants in Fig. 2. Fig. 2a plots the magnitude of the DAE as a function of the size of the DR, as well as the best-fitting regression line to the datapoints. DAEs and DR effects were calculated for each individual by subtracting baseline measurements of PSE from the PSE derived from test conditions with contextual modulation. The scatterplot clearly illustrates the high degree of interindividual variability in the magnitude of both effects, with effect sizes ranging by approximately 6° for both the DAE and DR. More pertinently, there was a strong significant positive correlation between these two effects ($r = 0.54$, $p < 0.0001$).

Fig. 2b plots the threshold data that accompanied the DAE as a function of thresholds from the DR task. Data are represented as threshold ratios, calculated by dividing thresholds obtained for conditions involving contextual modulation by baseline direction discrimination thresholds. Values greater than one indicate a cost in discriminative accuracy due to spatial or temporal contextual modulation, while values less than one denote an improvement. Plotted this way, it is clear that the vast majority of participants display threshold elevations in both spatial and temporal context conditions. While previous studies have shown that adaptation to motion directions away from the category boundary (e.g. upwards) lead to increases in discrimination thresholds (e.g. Hol & Treue, 2001; McGovern et al., 2012; Price & Prescott, 2012), to
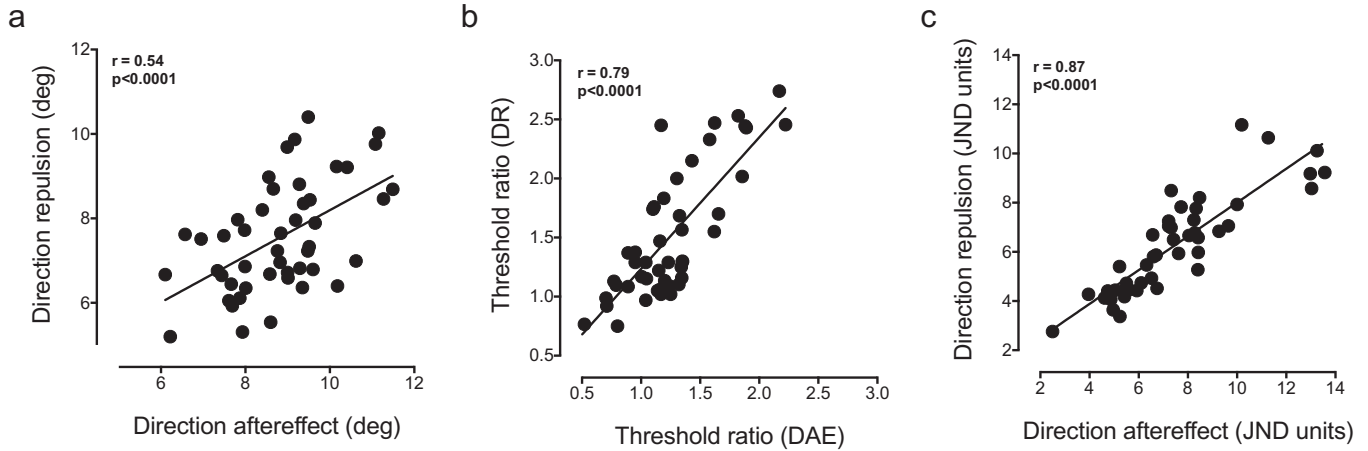
Fig. 2. Scatterplots, Pearson correlation coefficients and best-fitting regression line for the effects of spatial context on motion perception as function of temporal context effects. There was a strong positive correlation across participants for both (a) the magnitude of the DAE and DR, (b) as well as the threshold elevations induced by spatial and temporal context. This correlation was also evident when data were expressed in JND units (c).

our knowledge this is the first study to report a similar effect induced by a surrounding motion stimulus. Consistent with the bias data plotted in Fig. 2a, there was a strong positive correlation between the threshold ratios induced by the spatial and temporal context ($r = 0.79$, $p < 0.0001$). Given the similarity between the correlations for the bias and discrimination measures of the DAE and DR, we also plotted these data in JND units in Fig. 2c. Again, this plot demonstrates a strong relationship ($r = 0.87$, $p < 0.0001$) between the effects of spatial and temporal context on motion perception.

3.2. Relationship between direction and tilt aftereffects

The striking similarities between the effects of adaptation in both the orientation and motion domains has led to the suggestion that they share common computational principles (e.g. Clifford, 2002). To examine the relationship between the effects of orientation and motion adaptation, we also included a measure of the TAE in our test battery. Fig. 3 comprises three scatterplots displaying the effects of motion adaptation against those of orientation adaptation. Fig. 3a shows that there was weak positive correlation between the measures of the DAE and the TAE, however, this

correlation failed to reach statistical significance ($r = 0.31$, $p = 0.056$). A similar relationship was seen in the threshold data in Fig. 3b, although the correlation was weaker than that observed in the bias data ($r = 0.24$, $p = 0.18$). Finally, when expressed as JND units, there was a weak, non-significant correlation between the measures of orientation and motion adaptation ($r = 0.26$, $p = 0.14$).

3.3. Relationship between contrast adaptation and all other tasks

Fig. 4 shows three scatterplots in which the effects of contrast adaptation are plotted against all the other tasks in our test battery. Although contrast is likely to be encoded in a very different way to motion or orientation, we included the task to test for the possibility that participants might display a stereotyped level of adaptation across a range of stimulus properties. The measure of contrast adaptation was calculated by dividing the perceived contrast of the test Gabor patch following adaptation by the baseline measure of perceived contrast. As can be seen in the data plotted in Fig. 4, there was no relationship between this measure of contrast adaptation and either the DAE (Fig. 4a), DR (Fig. 4b) or the TAE (Fig. 4c).
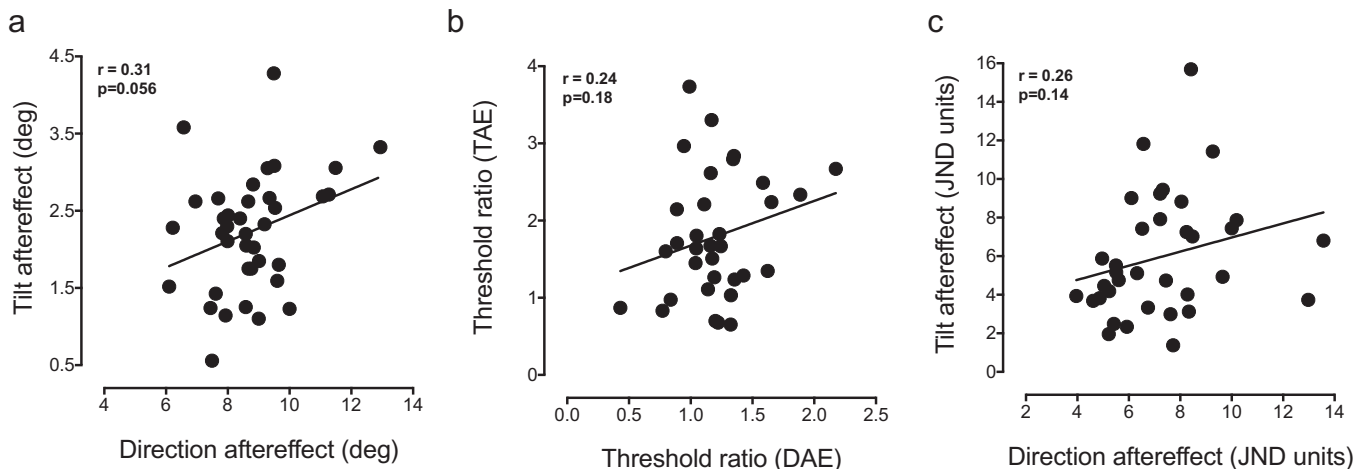

Fig. 3. Scatterplots, Pearson correlation coefficients and best-fitting regression line for the effects of adaptation on orientation and motion perception. (a) There was a weak positive correlation across participants for the magnitude of the DAE and TAE, although this did not reach statistical significance ($p = 0.056$). There was also weak, non-significant correlations between the threshold ratios measured from these tasks (b) and when data were expressed as JND units (c).
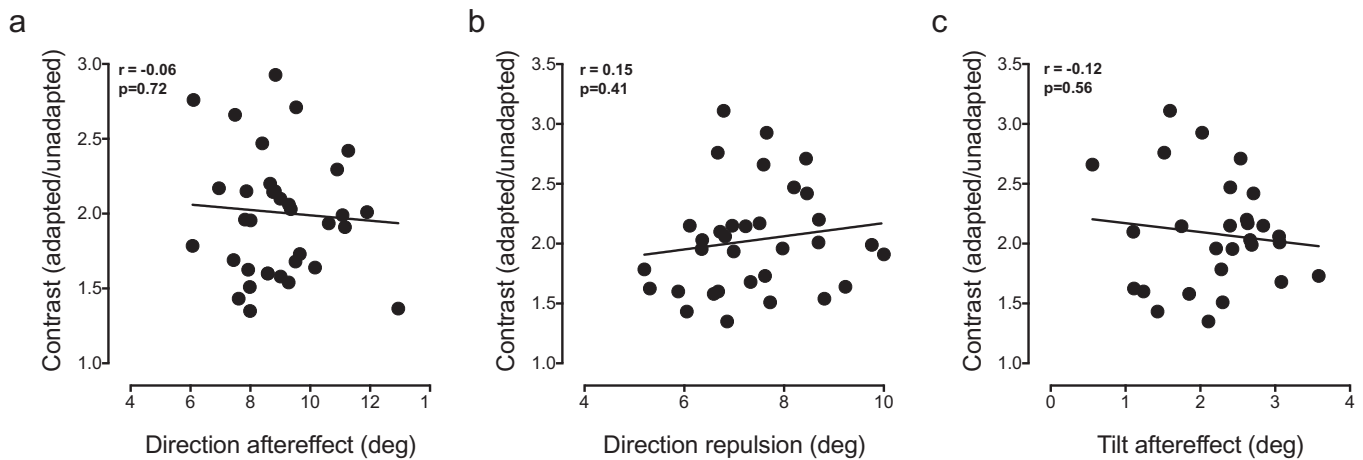
Fig. 4. Scatterplots, Pearson correlation coefficients and best fitting-regression lines for the effects of contrast adaptation against the effects from the other tasks in our test battery. There was no relationship between contrast adaptation effects and (a) the DAE, (b) DR or (c) the TAE.

4. Discussion

The similarity in the characteristics of spatial and temporal contextual modulation on visual perception has led to the suggestion that they arise from similar neural mechanisms (e.g. Schwartz et al., 2007). In particular, parallels have been drawn between the TAE and its simultaneous counterpart, the tilt illusion, owing to the similarities in their spatial tuning properties (Clifford et al., 2000; Magnussen & Kurtenbach, 1980; Wenderoth & Johnstone, 1988). The picture is less clear in the case of motion perception, however, where there is conflicting psychophysical evidence regarding the processing stages underlying the DAE and DR (e.g. Curran et al., 2006; Wiese & Wenderoth, 2007). Here we provide support for the view that these phenomena share common underlying mechanisms by showing that the magnitudes of these effects are strongly positively correlated across individuals. This positive correlation is present both in the repulsive shifts induced by spatial and temporal context, as well as in the cost for discriminative accuracy that accompany these context-dependent biases. By comparison, there was a weak correlation between the measures of the DAE and the TAE, while there was no relationship between contrast adaptation effects and the other context-dependent effects measured in our test battery.

Previous research has provided conflicting evidence regarding the neural origins of the DAE and DR. Evidence supporting the view that DR arises through local motion processing comes from studies in which the inducer and test stimuli were shown to different eyes (Grunewald, 2004; Wiese & Wenderoth, 2007, 2010). Whereas the DAE demonstrated robust interocular transfer (Wiese & Wenderoth, 2007), the magnitude of DR was significantly reduced with this stimulus arrangement (Wiese & Wenderoth, 2007, 2010), suggesting that it is at least partially mediated by monocular cells. Since monocularly driven neurons do not exist beyond primary visual cortex, these findings are consistent with the view that DR and the DAE are the result of activity at early and late stages of motion analysis, respectively. It should be noted, however, that others have shown robust interocular transfer of direction repulsion (Kim & Wilson, 1997), leading these authors to suggest that DR arises from activity in area MT. This argument is bolstered by evidence from studies employing mixed-speed inducer stimuli (Benton & Curran, 2003; Curran et al., 2006). Making use of the fact that DR and the DAE are tuned to differences in the speed between inducer and test stimuli (Curran & Benton, 2003; Dakin & Mareschal, 2000), these studies demonstrated that while the magnitude of DR was determined by the global speed of the inducing

stimulus (Benton & Curran, 2003), the DAE appeared to be driven by adaptation to the local motion component speeds (Curran et al., 2006). In an effort to reconcile these discrepant results, more recent accounts of the DAE and DR suggest that they could arise from neural interactions at both local and global motion processing stages (Farrell-Whelan et al., 2012; Wiese & Wenderoth, 2010). While our data do not provide insight as to the levels of cortical analyses involved in the DAE or DR, they do suggest that there is significant overlap in their processing.

Our data support the prevailing view that spatial and temporal contextual processes are designed to achieve common functional goals and are governed by similar computational principles (Clifford, 2014; Schwartz et al., 2007; Webster, 2014). However, questions remain as to the exact function of contextual modulation. This is largely due to the multitude of potential benefits associated with contextual modulation that have been reported in the literature including enhanced coding efficiency (Barlow, 1990; Clifford et al., 2000; Schwartz, Sejnowski, & Dayan, 2009; Schwartz et al., 2007), error-correction (Andrews, 1964; Anstis, Verstraten, & Mather, 1998; Ullman & Schechtman, 1982) and recalibration (Gibson, 1937; Solomon & Morgan, 2006). However, this broad range of benefits belies the fact that they are likely to be a consequence of a single type of adjustment in the visual system (Webster, 2014, 2015). There is converging evidence to suggest that this adjustment may take the form of divisive gain control, whereby the responses of sensory neurons are divided by the summed activity of populations of neurons coding for the same stimulus dimension (e.g. Carandini, Heeger, & Movshon, 1997; Schwartz et al., 2009; Webster, 2014). Gain control is an appealing candidate process as it appears to be a canonical computation in the brain, occurring in a range of different sensory modalities and brain regions (Carandini & Heeger, 2012), and it allows a system to be self-calibrating (Clifford, 2014). Furthermore, divisive gain control can explain the full range of effects of spatial contextual modulation, including repulsive and attractive biases in perception (Schwartz et al., 2009).

While we report a strong correlation between spatial and temporal contextual effects on motion perception, many studies employing an individual differences approach have failed to find a relationship between different measures of sensory performance. For instance, Goodbourn et al. (2012) tested four different tasks believed to probe magnocellular function in a large sample of participants (n = 1060) and showed that performance was only weakly correlated between tasks, with only one pair of tasks sharing more than 4% of variance. Similarly, Yazdani, Serrano-Pedraza,

Whittaker, Trevelyan, and Read (2015) reported no significant correlation between performance on two common psychophysical measures of surround suppression. Another study measured performance on six basic tests of visual performance and found only four significant correlations out of a possible 15, all of which had low correlation coefficients (Cappe, Clarke, Mohr, & Herzog, 2014). To explain these unexpectedly weak correlations, Cappe et al. suggested that individual differences across visual tasks could arise through everyday perceptual learning, whereby individual experience with the environment leads to specialised skills that do not transfer across tasks. While this may explain the weak correlations observed in their study, it is difficult to reconcile this argument with the finding reported here of a correlation between the effects of contextual modulation, since participants are likely to have unique experiences of spatial and temporal context. Rather, we take the view that the positive correlation between the DAE and DR is a result of the two effects sharing common mechanisms, while the tasks used in these aforementioned studies likely targeted distinct mechanisms.

Although it did not reach statistical significance, the weak correlation between the DAE and the TAE may be due to an overlap in the processing of orientation and motion. For instance, an established model of motion processing comprises two stages, corresponding to neurons located in primary visual cortex (V1) and area MT (Simoncelli & Heeger, 1998). In this model, V1 neurons encode both orientation and direction, while MT neurons process input from V1 to encode velocity (speed and direction). If we assume that the TAE arises through activity in V1, and the DAE arises from interactions in V1 and MT, we might expect these measures to be somewhat related. Furthermore, we suspect that the relationship between the DAE and TAE may be stronger than the current data suggest. Although participants were instructed to maintain fixation on the cross in the centre of the display for the duration of the experiment and their heads were stabilised in a chin-rest, small eye movements could affect the magnitude of the measured aftereffects. For instance, small eye movements could lead to the adaptor and test stimuli driving different neurons leading to attenuated aftereffects. Given the comparatively smaller receptive fields found in V1 relative to MT (Albright & Desimone, 1987), this is likely to be a bigger issue for the TAE and may have acted to introduce additional noise into our TAE measurement.

The effects of contrast adaptation did not correlate with those from any of the other tasks in the test battery. This was unsurprising as the encoding of contrast is very different from that of motion direction or orientation. While the responses of neurons generally increase monotonically with contrast (but see Peirce, 2007), motion and orientation are encoded by populations of neurons with different tuning preferences and unimodal tuning curves (e.g. Hubel & Wiesel, 1968). Despite these differences, we included the contrast adaptation task in the study to test the possibility that contextual modulation is governed by a global parameter, which controls the strength of all contextual effects arising from visual cortex. Since there was no relationship between the measure of contrast adaptation and the other tasks, we conclude that there is not one general mechanism that determines the magnitude of visual context-dependent effects. Rather, our finding of a strong positive correlation between the direction aftereffect and direction repulsion provides clear evidence for a common mechanism underlying the effects of spatial and temporal context on motion perception.

Acknowledgments

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