



# The relative contributions of global and local acceleration components on speed perception and discriminability following adaptation



Markus A. Hietanen\*

National Vision Research Institute, Australian College of Optometry, Cnr Cardigan and Keppel Street, Carlton, VIC 3053, Australia

ARC Centre of Excellence for Integrative Brain Function and Department of Optometry and Vision Sciences, University of Melbourne, Parkville, VIC 3010, Australia

## ARTICLE INFO

### Article history:

Received 30 April 2015

Received in revised form 12 June 2015

Accepted 23 June 2015

Available online 15 September 2015

### Keywords:

Speed

Velocity

Motion

Sensitivity

Adaptation

Discriminability

Perception

## ABSTRACT

The perception of speed is dependent on the history of previously presented speeds. Adaptation to a given speed regularly results in a reduction of perceived speed and an increase in speed discriminability and in certain circumstances can result in an increase in perceived speed. In order to determine the relative contributions of the local and global speed components on perceived speed, this experiment used expanding dot flow fields with accelerating (global), decelerating (global) and mixed accelerating/decelerating (local) speed patterns. Profound decreases in perceived speed are found when viewing low test speeds after adaptation to high speeds. Small increases in the perceived speed of high test speeds occur following adaptation to low speeds. There were small but significant differences in perceived stimulus speed after adaptation due to different acceleration profiles. No evidence for global modulation of speed discriminability following adaptation was found.

© 2015 Elsevier Ltd. All rights reserved.

## 1. Introduction

Our perception of speed following visual adaptation changes following visual motion adaptation. This generally presents as a reduction of the perceived speed of an image moving at a constant speed (Goldstein, 1957; Thompson, 1981) and an increase in sensitivity to changes in the relative speed of the stimulus (Bex, Bedingham, & Hammett, 1999; Clifford & Langley, 1996; Clifford & Wenderoth, 1999; Hietanen, Crowder, & Ibbotson, 2008; Krekelberg, van Wezel, & Albright, 2006). As the duration of the adaptation is increased, perceived speed tends to decrease in an exponential fashion (Bex, Bedingham, et al., 1999; Clifford & Langley, 1996; Goldstein, 1957; Hammett, Thompson, & Bedingham, 2000).

However, these changes in perceived speed following adaptation aren't always reductions, Smith and Edgar (1994) first showed that increases in the perceived speed of a translating drifting pattern depend upon the drift-rates presented prior to the test grating. Specifically, when test gratings drifted at or below the prior adaptation grating perceived drift-rates were below veridical perception, and when test gratings were faster than the adaptor perceived drift-rates were above veridical. Hammett, Champion,

Morland, and Thompson (2005) also examined drift rates following adaptation using drifting gratings and showed that adaptation reached its peak after 30 s of adaptation. These studies used single spatial frequency filter profiles, while psychophysical temporal filters are known to vary with spatial frequency (Anderson, 1985) and SF has effects on perceived speed (Campbell & Maffei, 1981; Smith & Edgar, 1991). Additionally, Bex, Metha, and Makous (1999b) found that motion aftereffects for radial stimuli were stronger than for translating stimuli. Hietanen et al. (2008) expanded these results using expanding random dot patterns. They showed that increases in the perceived speed of a fast stimulus can occur under conditions where the adaptation speed was far slower than the subsequent test. Hietanen et al. (2008) also demonstrated that adaptation was affected by the pattern of global speed, as adaptation was stronger for stimuli that accelerated towards the periphery in a flow field than for stimuli which travelled at a constant speed. They also demonstrated that speed discriminability was reduced following adaptation to low speeds when tested at high speeds, and increased when the test speed was at or below prior adaptation speeds.

As motion adaptation is a fundamental property of many of the neurons of the visual system (for review, Clifford & Ibbotson, 2003). Neural adaptation to moving stimuli presents as firing rate reductions during stimulation with a constant stimulus (Barlow & Hill, 1963). Adaptation can also be observed as a change in the sensitivity to stimuli presented after a period of constant stimulation

\* Address: National Vision Research Institute, Australian College of Optometry, Cnr Cardigan and Keppel Street, Carlton, VIC 3053, Australia.

E-mail address: [mhietanen@nvri.org.au](mailto:mhietanen@nvri.org.au)

(e.g. Greenlee & Heitger, 1988; Hietanen, Crowder, & Ibbotson, 2007; Hietanen et al., 2008). Maddess and Laughlin (1985) showed that an increase in sensitivity to changes around the presented speed (speed discriminability) occurs concurrently with reductions in the firing rate of motion sensitive neurons during adaptation to a moving patterns (also see Clifford, Ibbotson, & Langley, 1997; Clifford & Langley, 1996). Given that some motion sensitive neurons show similar reductions in absolute speed sensitivity and improvements in relative speed sensitivity (Clifford & Langley, 1996; Maddess & Laughlin, 1985) to that demonstrated psychophysically (Hietanen et al., 2008). The questions of why radial stimuli show stronger adaptation than translating stimuli (Bex et al., 1999); and why accelerating expanding stimuli show greater adaptation than constant speed stimuli (Hietanen et al., 2008) lead to several competing hypotheses: (1) the accelerating stimuli which consist of many different local velocities adapt more neurons than the constant speed stimuli, producing weaker adaptation; and (2) the accelerating stimulus produced stronger adaptation effects due to an inherent preference for expanding accelerating flow fields similar to that encountered during self-motion. This study expands on the previous work by Hietanen et al. (2008), investigating any differences in adaptation due to the speed of the elements in a flow field pattern, specifically between accelerating flow fields, decelerating flow fields and a mixed acceleration–deceleration condition to further explore how the visual system changes our perception of speed based on the pattern of global motion. In a related study Harvey and Braddick (2011) examined the relative contribution of local and global motion processing on the perception of pattern detection and position discrimination following adaptation. They found that when stimuli were tested using motion in the same direction as a prior adaptor there were no discernable differences that could be attributed to global motion processing. However when test stimuli moved in a direction opposite to the adaptor and the test stimulus was constructed to avoid local motion adaptation, global motion effects were detectable.

In the present study it was expected that, as in the previous study (Hietanen et al., 2008), when the adaptation speed is the same or faster than the test speed, there is a reduction in perceived speed relative to the speed presented. When the test speed is faster than the adaptation speed, perceived speed will be faster than veridical. It would also be expected that, if there is a global motion perception component to the increased adaptation that is specific to naturally occurring stimuli (such as expanding dot velocities matching those encountered during self-motion), perceived speed following adaptation will be stronger for accelerating (and potentially decelerating) stimuli than when both acceleration and deceleration are coincident. Conversely if the strength of adaptation is simply due to the local motion velocities in the stimulus then there should be no difference between the three speed profile conditions.

## 2. Methods

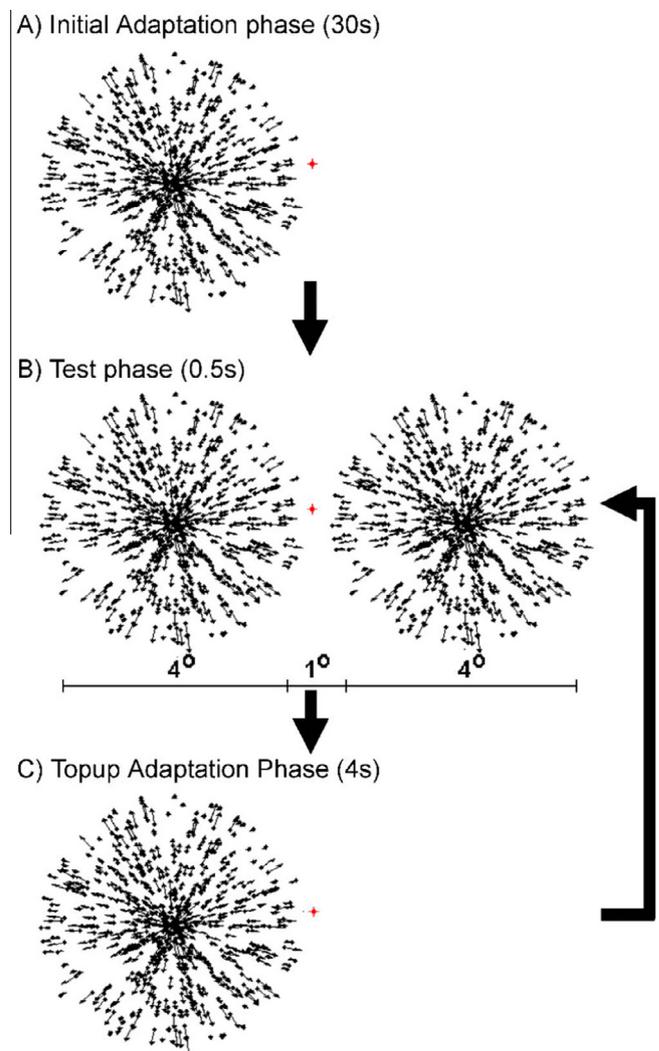
### 2.1. Subjects and equipment

Seven subjects (ages 22–28) participated in the study. All subjects had normal or corrected to normal vision. All subjects were naïve observers and provided informed consent, and the project was conducted in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). The stimuli were generated by a VSG 2/5 graphics card (Cambridge Research Systems Ltd.). Stimuli were presented on a calibrated 20 in. colour monitor (Eizo T662-T 1024 × 768 pixels, 400 × 300 mm) located 57 cm from the subject's eyes. Subjects were stabilized using a chin support. As in the prior study (Hietanen et al., 2008) the stimulus

consisted of two 4 degree diameter circular apertures located 2.5° on either side of a central fixation point.

In each of the two apertures were 200 dots positioned in random virtual 3D positions. Each dot had a maximum presentation period of 8 frames (80 ms) before it was replaced by a new randomly generated dot. To reduce stimulus temporally coherent flicker the dots were initially generated with a randomly generated time to live of 1–8 frames. Additionally, if a dot escaped the aperture of the stimulus it was immediately replaced with a new randomly generated dot. In all conditions there were 200 dots present in each aperture on every frame and so the root mean squared (RMS) contrast was constant though-out and between each stimulus presentation.

The temporal sequence of the stimulus (Fig. 1) consisted of an initial 30 s adaptation period during which an adaptation stimulus was presented in the left aperture. This was followed by a series of 40, 0.5 s test periods during which a test stimulus was presented in the left aperture and a matching stimulus was presented in the



**Fig. 1.** A schematic showing the temporal characteristics of the experimental protocol. (A) The adaptation stimulus consisted of random dots moving from the centre to the periphery for 30 s. The average instantaneous speed of the dots in the adaptation speed was constant at either (1.5, 6 or 24°/s). (B) The test phases (0.5 s) consisted of a test stimulus (LEFT) in which the average speed of the dots was constant at either (1.5, 6 or 24°/s) and a matching stimulus (RIGHT) in which the average speed of the dots was manipulated between trials to determine the perceived speed of the left aperture). (C) The adaptation stimulus was repeated for 4 s following each test phase (B).

right aperture. The global speed of the matching stimulus was determined using 2 independent QUEST staircases (Watson & Pelli, 1983) that converged on the perceived speed of the stimulus. Trial sets on which the two concurrently collected independent estimates of perceived speed differed by more than 10% were excluded and repeated at a later time. Following each test period subjects were required to indicate which stimulus “moved faster”, with a mouse click. Each 0.5 s test period was followed by a 4 s adaptation period in which the stimulus was identical to the initial adaptation period. The experiment consisted of 3 average adaptation speeds (1.5, 6, 24°/s), 3 test speeds (1.5, 6, 24°/s) and 3 unadapted controls in which the initial adaptation period was omitted and the top-up adaptation periods were replaced with a blank screen of mean luminance. A period of 10 min during which no testing was conducted was inserted between trial sets to ensure that prior periods of adaptation did not influence subsequent trials. The global pattern of dot speeds within in each aperture was manipulated to produce 3 conditions (Fig. 2): (1) in the acceleration condition the stimulus replicated the experiment presented by Hietanen et al. (2008) in which the dots accelerated from stationary at the centre towards the periphery; (2) a new deceleration condition in which the dots decelerated to stationary from the centre towards the periphery; and (3) a local motion condition in which each dot independently accelerated or decelerated from the centre to the periphery. Between conditions the instantaneous speeds of the dots in the stimulus were matched and only the polarity of acceleration was manipulated.

### 3. Results

Radially expanding flow fields of three different speed profiles were presented: (1) dots accelerating from the centre to the periphery; (2) dots decelerating from the centre to the periphery; and (3) dots either accelerating or decelerating from the centre to periphery (mixed condition). Subjects compared simultaneously presented stimuli on the left and right of a fixation point and reported the stimulus they perceived as moving faster.

#### 3.1. Changes in perceived speed following adaptation

The perceived speed of the stimulus was quantified as the point of subjective equality (PSE) between the speeds in the adapted and comparison apertures for each combination of adaptation speed, test speed, and speed profile. These PSEs were determined using 2 independent but concurrently iterated QUEST staircases. At least 4 PSEs were collected for each condition from each subject for each condition. A preliminary analysis of the PSEs collected revealed that one subject was producing inconsistent measures of perceived speed. Specifically, the PSEs for each of their concurrently collected independent QUEST staircases were not correlated and the standard errors associated with their PSEs were elevated by an order of magnitude compared to other subjects. For these reasons the data from this subject were deemed unreliable and excluded from further analysis.

The normalised change in perceived speed due to adaptation was calculated using the formula:

$$\text{Shift-in-PSE (sPSE)} = \frac{\text{PSE}_{ij} - \text{PSE}_{0j}}{\text{PSE}_{ij} + \text{PSE}_{0j}} \quad (1)$$

where,  $\text{PSE}_{ij}$  is the mean PSE following adaptation at a speed  $i$  and with a test speed  $j$ , and  $\text{PSE}_{0j}$  is the PSE speed in the non-adapted condition. Positive sPSE indicate increases in perceived speed, while negative sPSE indicate reductions in perceived speed, following adaptation.

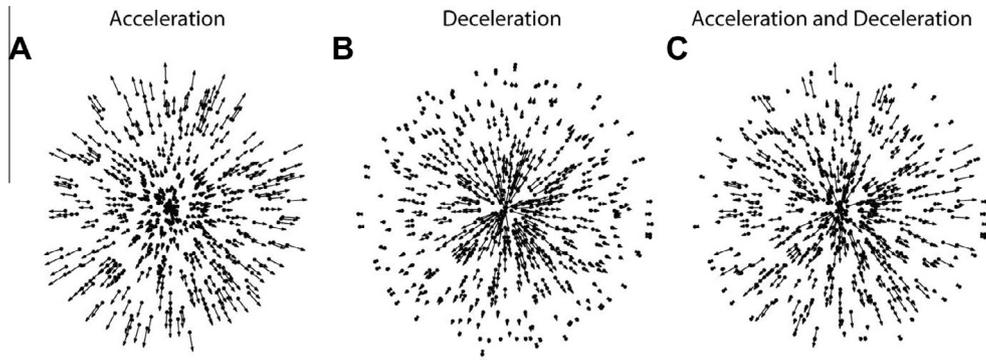
As the between-subject effects were so minimal, accounting for 4% of the total variability in the data, the mean sPSE (across all subjects) is presented as a function of adaptation speed, test speed and the speed profile of the stimulus as Fig. 3. Perceived speed was slower than veridical when the test speed was at or slower than the adaptation speed, and faster than veridical when test speed was much faster than the adaptation speed. To investigate the interaction between adaptation speed, test speed and the global speed pattern a 3-way repeated measures ANOVA was conducted examining the effects of adaptation speed, test speed and speed profile on the shift in PSE,  $F_{156,1045} = 68.212$ ,  $p < 0.0001$ . Experimental effects ( $\text{Eta}^2$ ) accounted for 85% of the variability in the data. As there was a significant 3-way interaction between adaptation speed, test speed and the speed profile of the stimulus,  $F_{8,40} = 31.31$ ,  $p < 0.001$ , the data from each speed profile was subsequently examined independently.

#### 3.2. Adaptation to accelerating stimuli

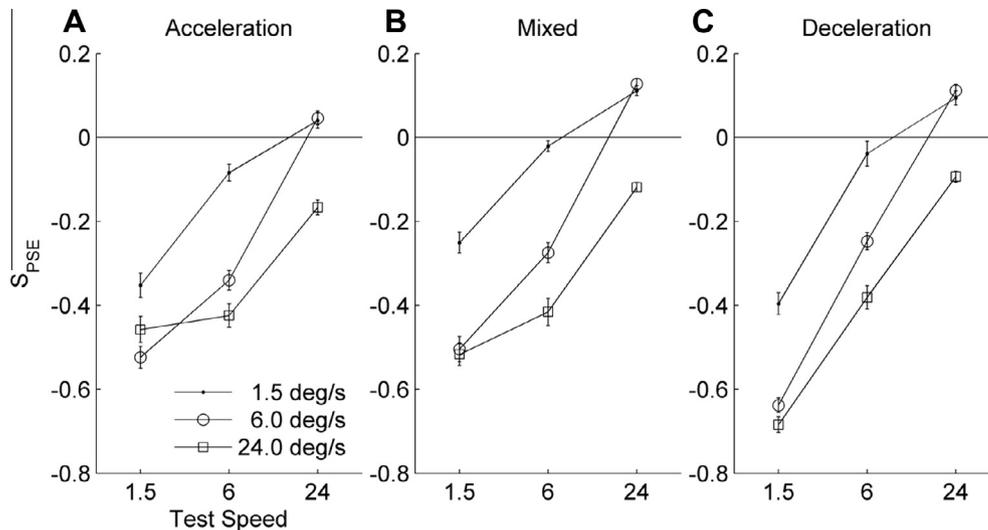
A 2-way repeated-measures ANOVA of the relationship between adaptation and test speeds on the shift-in-PSE was conducted for trials in which the stimulus was accelerating. There was a significant main effect of both adaptation speed demonstrating that the adaptation speed influenced the perceived speed of the stimulus ( $F_{2,10} = 17.79$ ,  $p < 0.001$ ). Additionally, test speed also changed the relative perceived speed of the stimulus ( $F_{2,10} = 35.79$ ,  $p < 0.0001$ ). Finally, there was a significant interaction between adaptation and tests speeds on the perceived speed of the stimulus ( $F_{4,322} = 24.25$ ,  $p < 0.0001$ ), indicating that the effect of test speed on the perceived speed was different depending on the adaptation speed that was presented. An analysis of the size of these effects using  $\text{Eta}^2$  demonstrated that adaptation speed, test speed and their interaction accounted for 14%, 46%, and 6% of the data respectively. In order to determine the nature of the interaction three 2D a-priori trend analyses were conducted considering whether: (1) sPSE changed log-linearly with adaptation speed regardless of the test speed,  $t = 7.62$ ,  $p < 0.001$ ; (2) sPSE changed log-linearly with test speed regardless of the adaptation speed,  $t = 6.88$ ,  $p < 0.001$ ; and (3) sPSE changed log-linearly with both adaptation speed and test speed,  $t = 7.7811$ ,  $p < 0.001$ ). These results replicated those found in Hietanen et al. (2008) in that perceived speed following adaptation for an accelerating flow field was best fit with log-linear relationships in both adaptation and test speeds. Specifically, perceived speeds are: slower than veridical when the test speeds were the same or slower than the adaptation speed; and faster than veridical when the test speeds were much faster than the adaptation speed, specifically when adaptation was at 1.5°/s and the test was at 24°/s.

#### 3.3. Adaptation to decelerating stimuli

Another 2-way repeated measures ANOVA and subsequent a-priori trend analyses were conducted for the deceleration condition. Between subject effects accounted for just 2% of the variability in sPSE. Similarly to the acceleration condition there were significant main effects of adaptation speed ( $F_{2,10} = 46.65$ ,  $p < 0.0001$ ), and test speed ( $F_{2,10} = 67.59$ ,  $p < 0.0001$ ) accounting for 12% and 65% of the variability in sPSE respectively. There was also a significant interaction between adaptation and test speed on sPSE ( $F_{4,322} = 27.49$ ,  $p < 0.0001$ ) that accounted for 4% of the variability in the data. Once again the 2D trend analyses revealed that the log-linear contributions of both adaptation and test speeds provided the best explanation for the shifts-in-PSE,  $t = 20.4$ ,  $p < 0.001$ , beating adaptation speed only  $t = 9.17$ ,  $p < 0.001$ , and test speed only,  $t = 8.21$ ,  $p < 0.001$ .



**Fig. 2.** A schematic of the stimulus speed of the random dot fields manipulated during the experiment. The length of the arrows represents the instantaneous speed of the dots at their relative positions. (A) Dots accelerated from stationary at the centre to a target speed in the periphery; (B) dots decelerated from the target speed in the centre to stationary at the periphery; (C) dots had independent local speed either accelerating as on the left or decelerating as in the centre.



**Fig. 3.** Average changes in perceived speed relative to veridical ( $sPSE$ ) for all subjects as a function of adaptation speed (symbol), and test speed (ordinate), for accelerating dots (A), mixed acceleration and deceleration (B) and decelerating dots (C). Generally speed profile had little effect on the perceived speed of the stimulus. Both adaptation speed and test speed had far more effect on  $sPSE$ . Perceived speed was slower than veridical when the test speed was at or slower than the adaptation speed, and faster than veridical when test speed was faster than the adaptation speed.

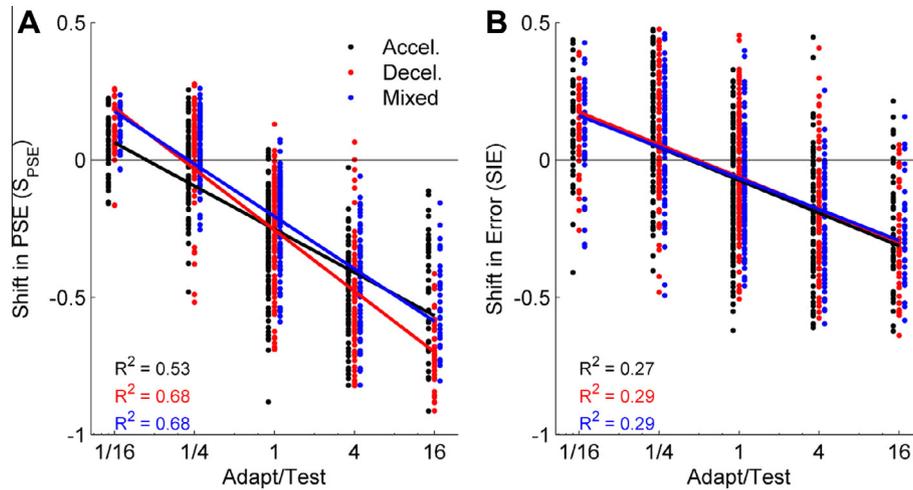
#### 3.4. Adaptation to mixed acceleration and deceleration

Finally, in contrast to the previous conditions that had coherent global motion profiles consisting of only accelerating or decelerating elements, a stimulus that consisted of independent accelerating and decelerating elements, was presented, producing a stimulus that would consist of largely local motion components. Again a 2-way repeated measures ANOVA was conducted, followed by a-priori trend analyses. The analysis revealed that there were significant main effects of adaptation speed ( $F_{2,10} = 178.08$ ,  $p < 0.0001$ ), and test speed ( $F_{2,10} = 39.03$ ,  $p < 0.0001$ ) accounting for 20% and 50% of the variability in  $sPSE$  respectively. There was also a significant interaction between adaptation and test speed on  $sPSE$  ( $F_{4,322} = 35.89$ ,  $p < 0.0001$ ) that accounted for 6% of the variability in the data. In contrast to the 2D trend analyses for the global acceleration and deceleration conditions, when the stimulus consisted of local motion components, the log-linear contribution of adaptation speed alone provided the best fit to the data,  $t = 9.17$ ,  $p < 0.001$ . The test speed only log-linear trend,  $t = 8.21$ ,  $p < 0.001$  and adaptation and test speed log-linear trend,  $t = 9.06$ ,  $p < 0.001$  were also significant.

#### 3.5. Comparison between speed profiles

The log-linear relationship between adaptation speed, and test speed was compressed into a single metric by examining the adapt/test speed ratio. The relationship between the adapt/test speed ratio and  $sPSE$  is shown as Fig. 4A for each of the dot speed profiles, averaged across all subjects. Colours in Fig. 4 represent the different speed profiles and the points have been artificially shifted slightly to allow comparison between conditions.

It is evident that when the dots are accelerating from centre to periphery the perceived speed of the stimulus is affected less by the adapt/test speed ratio than in the deceleration or mixed conditions. This results in smaller increases in perceived speed when adaptation speed is far lower than test speed (far left – black line) and smaller reductions in perceived speed when adaptation speed is far higher than test speed (far right – black line). Deceleration shows a steeper sloped relationship between adapt/test speed ratio and  $sPSE$  (red line), while the mixed condition falls somewhere between the other conditions. A 2 way ANOVA was conducted to determine the relative contributions of the adapt/test speed ratio, and the speed profile on the perceived speed of the stimulus ( $S_{PSE}$ ).



**Fig. 4.** (A) Shift-in-PSE as a function of the adaptation/test speed ratio, and speed profile (black – acceleration; red – deceleration; blue – mixed). When adaptation speed was equal to or higher than the subsequent test the perceived speed of the test stimulus was much slower than veridical. Conversely when the speed of the test stimulus was much higher than the adaptation stimulus the perceived speed of the test stimulus was slightly faster than veridical. These relationships were maintained across speed profiles and was slightly weaker for the accelerating stimuli than for the mixed or decelerating stimuli. (B) Shift-in-Error (SIE) as a function of the adaptation/test speed ratio, and speed profile (black – acceleration; red – deceleration; blue – mixed). Test speeds at or below the adaptation speed showed decreases in error (improved discriminability), testing at speeds far faster than the adaptation speed reduced speed discriminability. There were no differences in speed discriminability due to speed profile.

The results of the ANOVA reveal a significant 2-way interaction between the adaptation/test speed ratio and the speed profile,  $F_{8,1031} = 6.94$ ,  $p < 0.0001$ . The majority of the shift (measured using  $\text{Eta}^2$ ) in perceived speed following adaptation is due to the adaptation/test speed ratio,  $F_{4,1031} = 529.15$ ,  $p < 0.001$ , (65.3%) with the interaction  $F_{8,1031} = 6.94$ ,  $p < 0.0001$  (1.7%) and the speed profile,  $F_{2,1031} = 9.37$ ,  $p < 0.0001$  (5.8%) accounting for a further 7.5%. Comparisons of the  $S_{\text{PSE}}$  between speed profiles at each level of the adapt/test speed ratio were conducted using a Bonferroni corrected alpha level of (0.05/15),  $F_s > 5$ ,  $p < 0.0033$ . These comparisons revealed significantly lower  $S_{\text{PSE}}$  for the acceleration condition when compared to the mixed condition at adapt/test speed ratios of (1/16; 1/4; and 1). There were no significant differences between the 3 speed profiles at an adapt/test speed ratio of 4. There were significant differences between the deceleration condition and the acceleration and mixed conditions when the adapt/test speed ratio was 16 ( $F_s > 20$ ,  $p < 0.001$ ).

### 3.6. Changes in speed discriminability following adaptation

As in Hietanen et al. (2008) the present study sought to quantify the speed discriminability of the presented random dot stimuli. To quantify this a Shift-in-Error metric was calculated:

$$\text{Shift-in-Error (SIE)} = \frac{\text{EPS}_{ij} - \text{EPS}_{0i}}{\text{EPS}_{ij} + \text{EPS}_{0i}} \quad (2)$$

where  $\text{EPS}_{ij}$  is the standard error associated with the perceived speed following adaptation (as provided by the QUEST procedure) at speed  $i$  and with a comparison speed  $j$ , and  $\text{EPS}_{0i}$  is the error associated with the perceived speed in the non-adapted condition. Positive values of SIE are indicative of reduced discriminability while negative values indicate improved discriminability following adaptation.

A 3-way ANOVA examining SIE with adaptation speed, test speed and speed profile as the predictor variables was conducted. While the 3 way ANOVA showed that the 3 way interaction was significant,  $F_{8,40} = 5.842$ ,  $p < 0.0001$ , it also reveals that the speed profile (acceleration, deceleration and mixed) and all its interactions account for <2% of the total variance in the data ( $\text{Eta}^2$ ). Due to the small effect of Profile on the SIE a 2 way ANOVA, assuming

this simpler model without the Profile independent variable, was conducted. Due to the significant 2 way interaction between adaptation speed and test speed,  $F_{4,1012} = 14.137$ ,  $p < 0.0001$ , a 2D trend analysis was conducted and a significant log linear relationship between adaptation speed and test speed on the SIE was found to be the best predictor of SIE,  $t = 9.047$ ,  $p < 0.001$ . The relationship between the adapt/test speed ratio and SIE is shown as Fig. 4B for each of the dot speed profiles, averaged across all subjects. It is evident that there are no differences in speed discriminability due to the speed profile of the dots (lines from all speed profile conditions are parallel and coincident). This finding was confirmed using a 2 way ANOVA with adapt/test speed ratio and speed profile as predictors. The adapt/test speed ratio was a significant predictor of SIE ( $F_{4,1031} = 118.38$ ,  $p < 0.0001$ ), while speed profile and the interaction were not ( $F_{2,1031} < 1$  and  $F_{8,1031}$ ,  $p > 0.05$  respectively). As found in Hietanen et al. (2008), there is an increase in speed discriminability when adaptation speeds are far smaller than test speeds and speed discriminability is reduced when adapt and test speeds are similar to each other or when adaptation speeds are higher than test speeds.

## 4. Discussion

These results reinforce the common finding that perceived speed is reduced following adaptation to motion (Thompson, 1981; Hietanen et al., 2008; Krekelberg et al., 2006). Additionally further evidence of the less widely studied result that the perceived speed of a stimulus can actually increase when the speed of a test stimulus is much faster than the preceding adaptation stimulus (Hammett et al., 2005; Hietanen et al., 2008; Smith & Edgar, 1994). Hietanen et al. (2008) demonstrated that expanding global dot motion patterns with an accelerating component to the motion produced stronger adaptation (larger changes in perceived speed) than stimuli that consisted of only a single speed. They speculated that the increased strength of adaptation could have been due to acceleration sensitive neurons. Morrone et al. (2000) demonstrated using fMRI that a portion of primate V5/MT was devoted to complex motion such as radial motion. Similarly, Area V6 has been demonstrated to be sensitive to motion consistent

with self-motion (Cardin & Smith, 2010; Pitzalis et al., 2010). However, studies of area MT in macaques found no evidence of an acceleration signal in the neural responses (Price, Crowder, Hietanen, & Ibbotson, 2006), although an acceleration signal can be reconstructed from the speed tuned cells in MT if their transient responses were taken into account (Lisberger & Movshon, 1999). Schlack, Kregelberg, and Albright (2007) showed that the speed tuning of neurons in the MT of macaques changes dependent on whether a stimulus is accelerating or decelerating. They demonstrate that acceleration can be represented by speed sensitive cells without needing cells explicitly tuned to acceleration. In a subsequent study Schlack, Kregelberg, and Albright (2008) found that the speed history of accelerating or decelerating dots influenced the perceived speed after short 1 s periods of adaptation. Unfortunately, their study and the present study are not directly comparable as they included a 500 ms period of constant stimuli between the acceleration/deceleration and the test. Nevertheless, they found that perceived speeds following acceleration introduced larger reductions in perceived speed and increases in speed discriminability compared to deceleration. Two further explanations for the results of Hietanen et al. (2008) are: (1) as the accelerating stimulus approximated that of a flow field such as would be encountered during forward self-motion, the visual system may be selectively sensitive to these flow fields compared to the less commonly encountered constant speed expanding stimulus; or (2) as the dots accelerated they recruited a wider range of neurons throughout the visual system with a larger range of speed preferences and the increased adaptation to accelerating stimuli results from adapting more cells in total.

In support of the first hypothesis: from a perceptual standpoint there is ample evidence that complex (radial) stimuli are processed differently to simple stimuli (Regan & Beverley, 1979; Snowden & Milne, 1996, 1997; Morrone, Burr, & Vaina, 1995; Burr, Morrone, & Vaina, 1998; Morrone, Burr, Di Pietro, & Stefanelli, 1999; Bex et al., 1999). This is complemented by physiological studies showing that neurons in the visual cortex of primates, particularly areas MT (Mikami, Newsome, & Wurtz, 1986; Saito, Yukie, Hikosaka, Fukada, & Iwai, 1986) and MST (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Saito et al., 1986; Tanaka, Fukada, & Saito, 1989; Britten & van Wezel, 1998) have strong sensitivity to complex motion (e.g. rotation and radial). While the present study didn't examine patterns other than radial expansion, it did present several different stimuli that should be processed differently by cells tuned for global motion patterns approximating those found during self-motion. Stimuli in which the instantaneous dot velocities of each of the dots were matched, were presented, while the global relationship between the dot velocities varied between the acceleration, deceleration and mixed conditions. If the first hypothesis were to be supported it would be expected that there should be significant changes between the 3 acceleration profiles. While there were significant differences in the perception of speed following adaptation to the radial patterns with different speed profiles, these differences were small accounting for at most 6% of the change in perceived speed. As such, the present study tends to support the second of the two hypotheses outlined above: the adaptation effects seen in the perceived speed of radially expanding stimuli are largely determined by the local components that constitute them rather than the global structure of the stimulus. This is particularly the case when considering the speed discriminability results where there were essentially no differences in speed discriminability due to the global spatial structure of the stimuli following adaptation. This concurs with other studies that have shown that local global pattern learning is based on local motion (Nishina, Kawato, & Watanabe, 2009), and that global speed processing is dependent on local speeds rather than global speed (Khuu & Badcock, 2002).

However, as there was a significant (but small) difference in perceived speed that could be explained by the speed profile of the stimulus, it is not appropriate to reject the hypothesis that global motion has some effect on perceived speed following adaptation. The present study examined a specific set of global speed patterns (consistent acceleration and/or deceleration of expanding dots). It is possible that stimuli that comprise different subsets of global motion such as dots with random speed perturbations or concurrent accelerating and constant speed flow fields may effect perceived speed and speed discriminability in ways that are not within the scope of the present study. For example while driving with other vehicles in traffic, parts of the flow field may be obscured by other cars and local fluctuations in speed in different areas of the flow field will occur. Future research, could examine the relationship between the global perception of speed and spatially localised regions of constant or fluctuating speed profiles to determine whether there is any effect of spatial separation of local components on the global speed percept. Furthermore the present study is concerned with how adaptation changes our perception of speed and speed discriminability, without specific consideration of whether different velocity profiles, beyond those tested in the present study, have different thresholds for discriminability. Future research could examine the discriminability of the speed of a wider variety of flow fields, including those not consistent with self-motion, prior to adaptation and then determine if adaptation influences speed perception consistently across this larger subset.

## 5. Conclusions

Visual speed perception and speed discriminability, following adaptation, are largely determined by the ratio of current speeds to prior speeds. This relationship is largely dependent on the speeds of local motion components in the scene being viewed rather than the global relationship between the speeds of the local components. However the global relationship between the speeds of individual components does account for a small proportion (6%) of the variability in perceived speed following adaptation.

## Acknowledgments

The author would like to thank Prof Michael Ibbotson, Dr Josephine Battista and Dr Shaun Cloherty for their comments on an early version of this manuscript. This work was supported by Grants from the Australian Research Council: (1) Centre for Excellence in Vision Science (CE0561903), & (2) Centre of Excellence for Integrative Brain Function (CE140100007).

## References

- Anderson, S. J. (1985). Spatial and temporal selectivity of the human motion detection system. *Vision Research*, 25, 1147–1154 [PubMed].
- Barlow, H. B., & Hill, R. M. (1963). Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature*, 200, 1345–1347 [PubMed].
- Bex, P. J., Bedingham, S., & Hammett, S. T. (1999). Apparent speed and speed sensitivity during adaptation to motion. *Journal of the Optical Society of America A*, 16, 2817–2824 [Article].
- Bex, P. J., Metha, A. B., & Makous, W. (1999b). Enhanced motion aftereffect for complex motions. *Vision Research*, 39, 2229–2238 [PubMed].
- Burr, D. C., Morrone, M. C., & Vaina, L. (1998). Large receptive fields for optic flow direction in humans. *Vision Research*, 38, 1731–1743 [Article].
- Britten, K. J., & van Wezel, R. J. (1998). Electrical microstimulation of cortical area MST biases heading perception in monkeys. *Nature Neuroscience*, 1, 59–63 [Article].
- Campbell, F. W., & Maffei, L. (1981). The influence of spatial frequency and contrast on the perception of moving patterns. *Vision Research*, 21, 713–721 [PubMed].
- Cardin, V., & Smith, A. T. (2010). Sensitivity of human visual and vestibular cortical regions to ego motion-compatible visual stimulation. *Cerebral Cortex*, 20(8), 1964–1967 [Article].

- Clifford, C. W., Ibbotson, M. R., & Langley, K. (1997). An adaptive Reichardt detector model of motion adaptation in insects and mammals. *Visual Neuroscience*, 14, 741–749 [PubMed].
- Clifford, C. W., & Ibbotson, M. R. (2003). Fundamental mechanisms of visual motion detection: Models, cells and functions. *Progress in Neurobiology*, 68, 409–437 [PubMed].
- Clifford, C. W., & Langley, K. (1996). Psychophysics of motion adaptation parallels insect electrophysiology. *Current Biology*, 6, 1340–1342 [PubMed].
- Clifford, C. W., & Wenderoth, P. (1999). Adaptation to temporal modulation can enhance differential speed sensitivity. *Vision Research*, 39, 4324–4332.
- Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large field stimuli. *Journal of Neurophysiology*, 65, 1329–1345.
- Goldstein, A. G. (1957). Judgments of visual velocity as a function of length of observation time. *Journal of Experimental Psychology*, 54, 457–461 [PubMed].
- Graziano, M. S. A., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *Journal of Neuroscience*, 14, 54–67 [PubMed].
- Greenlee, M. W., & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Research*, 28(7), 791–797 [PubMed].
- Hammett, S. T., Champion, R. A., Morland, A. B., & Thompson, P. G. (2005). A ratio model of perceived speed in the human visual system. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2351–2356 [PubMed, Article].
- Hammett, S. T., Thompson, P. G., & Bedingham, S. (2000). The dynamics of velocity adaptation in human vision. *Current Biology*, 10, 1123–1126.
- Harvey, B. M., & Braddick, O. J. (2011). Similar adaptation effects on motion pattern detection and position discrimination tasks: Unusual properties of global and local level motion adaptation. *Vision Research*, 51, 479–488 [PubMed].
- Hietanen, M. A., Crowder, N. A., & Ibbotson, M. R. (2007). Contrast gain control is drift-rate dependent: An informational analysis. *Journal of Neurophysiology*, 97, 1078–1087 [PubMed].
- Hietanen, M. A., Crowder, N. A., & Ibbotson, M. R. (2008). Differential changes in human perception of speed due to motion adaptation. *Journal of Vision*, 8(11), 1–10. 6.1–10 [PubMed].
- Khuu, S. K., & Badcock, D. R. (2002). Global speed processing: Evidence for local averaging within, but not across two speed ranges. *Vision Research*, 42(28), 3031–3042 [PubMed].
- Krekelberg, B., van Wezel, R. J., & Albright, T. D. (2006). Adaptation in macaque MT reduces perceived speed and improves speed sensitivity. *Journal of Neurophysiology*, 95, 255–270 [PubMed].
- Lisberger, S. G., & Movshon, J. A. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *Journal of Neuroscience*, 19(6), 2224–2246 [PubMed].
- Maddess, T., & Laughlin, S. B. (1985). Adaptation of the motion-sensitive neuron H1 is generated locally and governed by contrast frequency. *Proceedings of the Royal Society of London B Biology*, 225, 251–275 [PubMed].
- Mikami, A., Newsome, W. T., & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *Journal of Neurophysiology*, 55, 1308–1327 [PubMed].
- Morrone, M. C., Burr, D. C., & Vaina, L. (1995). Two stages of visual processing for radial and circular motion. *Nature*, 376, 507–509 [PubMed].
- Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for visual optic flow. *Current Biology*, 9, 763–766 [PubMed].
- Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience*, 3, 1322–1328 [PubMed].
- Nishina, S., Kawato, M., & Watanabe, T. (2009). Perceptual learning of global pattern motion occurs on the basis of local motion. *Journal of Vision*, 28(9), 1–6. 15.1–6 [Article].
- Pitzalis, S., Sereno, M. I., Committeri, G., Fattori, P., Galati, G., Patria, F., et al. (2010). Human v6: The medial motion area. *Cerebral Cortex*, 20(2), 411–424 [PubMed].
- Price, N. S. C., Crowder, N. A., Hietanen, M. A., & Ibbotson, M. R. (2006). Neurons in V1, V2 and PMLS of cat cortex are speed tuned but not acceleration tuned: the influence of motion adaptation. *Journal of Neurophysiology*, 95(2), 660–673.
- Regan, D., & Beverley, K. I. (1979). Visually guided locomotion: Psychophysical evidence for a neural mechanism sensitive to flow patterns. *Science*, 205, 311–313 [PubMed].
- Saito, H. A., Yukie, M., Hikosaka, L., Fukada, Y., & Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *Journal of Neuroscience*, 7, 177–191 [PubMed].
- Schlack, A., Krekelberg, B., & Albright, T. D. (2007). Recent history of stimulus speeds affects the speed tuning of neurons in area MT. *Journal of Neuroscience*, 27(41), 11009–11018 [PubMed].
- Schlack, A., Krekelberg, B., & Albright, T. D. (2008). Speed perception during acceleration and deceleration. *Journal of Vision*, 8(8), 1–11. 9.1–11 [Article].
- Smith, A. T., & Edgar, G. K. (1991). The separability of temporal frequency and velocity. *Vision Research*, 31, 321–326 [PubMed].
- Smith, A. T., & Edgar, G. K. (1994). Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Research*, 34, 253–265 [PubMed].
- Snowden, R. J., & Milne, A. B. (1996). The effects of adapting to complex motions: Position invariance and tuning to spiral motions. *Journal of Cognitive Neuroscience*, 8, 435–455 [PubMed].
- Snowden, R. J., & Milne, A. B. (1997). Phantom motion aftereffects: Evidence of detectors for the analysis of optic flow. *Current Biology*, 7, 717–722 [PubMed].
- Tanaka, K., Fukada, Y., & Saito, H. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the MST area of the macaque monkey. *Journal of Neurophysiology*, 62, 642–656 [PubMed].
- Thompson, P. (1981). Velocity after-effects: The effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli. *Vision Research*, 21, 337–345.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics*, 33, 113–120 [PubMed].