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Dynamics of walking adaptation aftereffects induced in static images of walking actors

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ABSTRACT

Visual adaptation to walking actions results in subsequent aftereffects that bias perception of static images of walkers in different postures so that they are interpreted as walking in the opposite direction to the adapting actor. It is not clear, however, if the walking aftereffect is comparable to other well studied low- and high-level visual aftereffects. We therefore measured the dynamics of the walking aftereffect in order to assess the characteristics of the adapting mechanism. We found that walking aftereffects showed similar characteristic dynamics as for face aftereffects and some motion aftereffects. Walking aftereffects could be induced in a broad range of different static images of walking actors and were not restricted to images of actors in any particular posture. Walking aftereffects increased with adapting stimulus repetition and declined over time. The duration of the aftereffect was dependent upon time spent observing the adapting stimulus and could be well modelled by a power-law function that characterises this relationship in both face and motion aftereffects. Increasing the speed of the adapting stimulus by increasing actor walk speed increased aftereffect magnitude, as seen for some motion aftereffects. The nature of the aftereffects induced by observing walking actors indicates that they behave like traditional high-level visual aftereffects.

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1. Introduction

Visual adaptation occurs after prolonged exposure to almost any visual stimulus, resulting in aftereffects, or biases, in visual perception. These aftereffects can occur after exposure to simple geometric stimuli (e.g. Gibson & Radner, 1937; McCullough, 1965; Thompson, 1981) and complex social stimuli such as faces (e.g. Leopold et al., 2001; Rhodes et al., 2003; Webster & MacLin, 1999) and actions (e.g. Barraclough & Jellema, 2011; Barraclough et al., 2009; Troje et al., 2006), as well as complex natural scenes (Greene & Oliva, 2010).

Action adaptation has shown that visual adaptation occurs at a high-level in the visual system (Barraclough & Jellema, 2011; Barraclough et al., 2009; Lorteije et al., 2007). Although these studies could not rule out adaptation simultaneously occurring at a low-level in the visual system, adaptation to the simple visual characteristics of the stimuli could not explain the observed effects. High-level adaptation is likely to be responsible and occurring at a level in the visual system at which the goal-directed actions themselves are coded, for example in the Superior Temporal Sulcus (STS, Oram & Perrett, 1996; Perrett et al., 1989). Adaptation techniques were therefore used to infer the characteristics of the underlying action processing mechanisms without recourse to human neuroimaging techniques or invasive single unit recording in primates. Indeed, the mechanisms determined using psychophysical adaptation techniques in humans often show striking parallels with action coding mechanisms determined using single cell recording in the monkey. For example, visual adaptation showed that mechanisms processing walking actions were effectively "blind" to both the view and identity of the actor (Barraclough & Jellema, 2011) corroborating studies demonstrating similar coding properties in single units in the monkey (e.g. Jellema & Perrett, 2006).

A further characteristic of action processing mechanisms illustrated by adaptation studies has been the joint coding of stimuli containing motion information and static stimuli "implying" motion (Barraclough & Jellema, 2011; Winawer, Huk, & Boroditsky, 2008). Static pictures of humans, animals and objects in motion can imply a vivid sense of motion, often in a specific direction, despite the lack of any physical motion in the stimulus itself. In Barraclough and Jellema's (2011) study, adapting to movies of walking actors caused subsequent biases in the perception of static images of actors in different walking postures such that they were interpreted as implying motion in the opposite direction. Whilst Winawer, Huk, and Boroditsky (2008) demonstrated that adaptation to static images implying motion generated biases in the perception of moving dot fields. Neuroimaging studies have shown that motion processing areas are sensitive to static images of actors

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implying motion (Kourtzi & Kanwisher, 2000; Senior et al., 2000), furthermore, single cells in monkey STS that respond to walking actions will also respond to static images of actors implying motion (Barraclough et al., 2006; Vangeneugden et al., 2011). So, converging evidence from psychophysical adaptation, human neuroimaging and monkey neurophysiology studies indicate the joint coding of implied motion and physical motion.

It is not clear, however, if walking aftereffects (WAEs) as demonstrated by Barraclough and Jellema (2011), are equivalent to more commonly studied adaptation aftereffects, specifically face aftereffects and motion aftereffects (MAEs). Several different MAEs have been demonstrated and their characteristics are dependent upon the form of the adapting and test stimuli. Substantive differences are seen in MAEs induced in static or moving stimuli (e.g. Hiris & Blake, 1992; Verstraten, van der Smagt, & van den Grind, 1998). In the WAE the adapting stimulus is moving, and the test stimulus a static image of an actor; the WAE therefore more closely parallels, and is better compared to, the MAE induced in a static image. The relationship between the perceptual phenomena of the MAE and the underlying neurophysiological processes has been well characterised over many years (e.g. see Mather et al. (2008) for a review). In contrast, it is less understood how face perception aftereffects relate to changes in neural responses (Barraclough & Perrett, 2011). The acceptance, however, of face adaptation aftereffects as genuine high-level visual aftereffects, as opposed to reflecting alternate perceptual or cognitive mechanisms has relied upon comparisons of the characteristic dynamics of face aftereffects with those observed with more simple stimuli (Leopold et al., 2005; Rhodes et al., 2007), although see (Dickinson et al., 2010) for evidence that some face aftereffects can result from adaptation at a low level in the visual system. In the current study we therefore measured the dynamics of the WAE in order to establish whether it is comparable to other well-known aftereffects (MAE and face adaptation aftereffects), and assess whether adaptation at this late stage in visual processing shows similar characteristics.

Adaptation aftereffects show some characteristic properties that can distinguish them from other simultaneously acting perceptual mechanisms. First, adaptation typically results in aftereffects that look *less* like the adapting stimulus, a 'repulsive' effect. This is unlike a priming mechanism, a form of implicit memory, where stimuli look *more* like the preceding priming stimulus (e.g. Tulving & Schacter, 1990). Although the repulsive aftereffect is almost always observed when using typically constructed adaptation paradigms, occasionally *attractive* aftereffects have been observed under specific conditions, for example, following very brief adaptation and after longer intervals (e.g. Kanai & Verstraten, 2005). Second, adaptation aftereffects increase in a logarithmic fashion as the duration or repetition of the adapting stimulus is increased (e.g. Hershenson, 1989). This distinguishes adaptation from priming where single and repeated presentation of priming stimuli can result in similar functional changes (Schacter & Buckner, 1998). Third, aftereffect magnitude decays logarithmically with time (e.g. Hershenson, 1989; Kloth & Schweinberger, 2008; Leopold et al., 2005; Magnussen & Johnsen, 1986). The duration of the adaptation aftereffect can be quite variable, and is dependent also upon the duration of the adapting stimulus (e.g. Hershenson, 1989, 1993), but is in the order of a few seconds to a few minutes, distinguishing it from both forward masking and priming. Although forward masking shares some characteristics with adaptation, for example a repulsive effect and a decline during the interval between adapting/masking stimulus and the test stimulus, forward masking, however, only lasts a few 100s of milliseconds (e.g. Macknik & Livingstone, 1998; Perrett et al., 2009). Visual object priming, in contrast can last at least up to 6 weeks (Mitchell & Brown, 1988). We, therefore, tested both the build up of the WAE with adaptation duration and the decline of the aftereffect with time in order to compare with the dynamics of the previously assessed MAE (Hershenson, 1989, 1993) and face adaptation aftereffect (Leopold et al., 2005; Rhodes et al., 2007).

As it is possible to walk at varying speeds, we also wanted to test the effect of walker speed on the WAE. Previous measures of the speed tuning of the MAE induced in static stimuli have shown different results dependent upon the forms of the adapting and test stimuli. With simple translating gratings and rotating disks, increasing adaptor speed can increase the magnitude of the perceived aftereffect (Hershenson, 1989, 1993; Taylor, 1963). Other estimates suggest that MAE magnitude can be described as an inverted U-shape function (e.g. Verstraten, van der Smagt, & van den Grind, 1998), where, at high speeds, the MAE eventually declines again. Differences between the MAE and WAE precluded precise predictions for the WAE speed tuning function; however, we expected that speed would have a role in modulating the WAE magnitude. We, therefore, examined how adapting stimuli moving at different speeds influenced the WAE magnitude. We also tested the interaction between adapting walker speed and the duration of observation of the adapting walker. Combinations of walker speed and stimulus duration have the same number of walking cycles; therefore it was possible to compare aftereffect magnitude when the number of walking cycles was fixed in order to test the relative influence of adapting stimulus speed and adapting stimulus duration.

2. General methods

2.1. Participants

Participants in all experiments were University of Hull students and staff; students either received course credit or were paid for participating. All participants had normal or corrected-to-normal vision. Experiments were approved by the ethics committee of the Department of Psychology, University of Hull, and performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

2.2. Stimuli

One male actor was filmed walking forward to the left, orthogonal to the camera (Canon XL1s). Film clips (without video compression) were edited to isolate one walking cycle (left foot down to left foot down); each film lasted 28 frames (duration 1120 ms, 40 ms/frame). In each frame the background was coloured mid grey and the human body was centred in the horizontal plane so that the actor appeared to walk on a treadmill with no overall body translation. This restricted the recognition of the walking compatibility (forward/backward walking) to the articulatory movements of the actor, rather than a simple comparison between body translation and body view.

This film was used to generate all stimuli. The film was played backwards to generate backwards walking (in unpublished work we found that walking aftereffects generated from genuine backwards walking film and reversed forward walking film were equivalent, Barraclough and Jellema). Playing all frames from one film generated one walking cycle; playing a film n number of times generated n cycles of walking. Films were used as adapting stimuli; individual frames taken from the films were used as test stimuli.

2.3. Experimental procedure

A PC running MATLAB 2006a and the Cogent toolbox was used to control experiments, display stimuli (22.3 deg $\times$ 16.6 deg at the eye) on a 22″ flat screen CRT monitor (Philips 202P40,

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1600 × 1200 pixels, 100 Hz refresh rate), and record participant responses. Stimuli were presented in the centre of the screen, and so that the walking actor appeared 6.68 deg high and the maximum horizontal extent of the actor when in the most articulated pose was 3.80 deg.

Experiments followed the same general procedure as used in previous experiments (Barraclough & Jellema, 2011). Briefly, on each trial, participants viewed an adapting stimulus (either forward or backward walking) followed by a short inter-stimulus interval (ISI) and then a static test image taken from the film of the walking actor (80 ms duration). Participants were told that the image was of either the actor walking forward or backward and that they had to indicate the direction of walking on the computer keyboard. After the participant had indicated their response, the screen remained blank (grey) for 4000 ms before the start of the next trial.

Participant responses to test stimuli were scored either as 0 indicating a test stimulus was interpreted as walking backwards, or 1 indicating a test stimulus was interpreted as walking forward; mean participant responses to test stimuli were calculated and could vary between values of 0 and 1. Walking aftereffects were calculated separately for each participant and experimental condition by subtracting the mean response to the test stimuli following forward adaptation from the mean response to the test stimuli following backward adaptation; walking aftereffect values could vary between −1 and 1. Positive values indicated that the adapting stimulus had a *repulsive* effect where test stimuli appeared less like the adapting stimulus (as commonly observed during adaptation experiments). Negative values indicated that the adapting stimulus had an *attractive* effect where the test stimuli appeared more like the adapting stimulus. Large differences between judgments of test stimuli following forward and backward adapting stimuli indicate large aftereffects.

3. Experiment 1

3.1. Methods

Previously measured WAEs have only been tested within a restricted subset of images of walkers in different postures (Barraclough & Jellema, 2011) and WAE magnitude proved to be variable with different test stimuli. The WAE could, in principle, represent a change in the perception of walkers only in specific postures, for example, actors in either articulated or standing postures; furthermore, adaptation may result from a shift in the perceived degree of articulation of the static actor and hence potentially bias perceived direction of motion. We, therefore, in Experiment 1 tested the magnitude of the walking aftereffect for all possible test stimuli taken from the frames of the movie of the walking actor. We wanted to know if the walking aftereffect was present across all test stimuli, and whether there was any systematic bias across images of walkers in different articulated postures.

Fifteen participants (11 female and 4 male; mean age = 22.7 years, *SD* = 4.8 years) took part in Experiment 1; all participants, except the author JI, were naive to the purpose of the study. Adapting stimuli consisted of the film of the walking actor played forward 8 times, backward 8 times, or 8 repeats of a Fourier phases-scrambled (Nelissen, Vanduffel, & Orban, 2006) version of the film of the walking actor that contained many of the low level visual properties of the walking film (e.g. luminance, contrast, colour, spatial frequency), however the action itself could not be seen. Test stimuli were presented for 80 ms and consisted of the 28 different frames from the walking film. Each condition (test stimulus and adaptation stimulus combination) occurred 3 times in total and was presented in a pseudorandom manner (in total 252 trials: 28 test stimuli × 3 adapting stimuli × 3 trials/condition). Mean responses to each condition were calculated for each participant.

3.2. Results

As seen in previous research (Barraclough & Jellema, 2011) participant ratings of test stimuli were variable, however, they were significantly different under the different adapting conditions (see Fig. 1). A one-way analysis of variance (ANOVA; levels: after control adaptation, after forward adaptation, after backward adaptation) revealed a main effect of adaptation, $F(2,28) = 11.25$, $p < 0.0001$, $\eta_p^2 = 0.47$. Planned contrasts indicated that after adapting to a movie of an actor walking backward, participants were significantly more likely to interpret the test stimuli as walking forward: backward adaptation ($M = 0.79$, $SD = 0.14$) compared with control adaptation ($M = 0.65$, $SD = 0.20$), $F(1,14) = 14.24$, $p < 0.005$, $\eta_p^2 = 0.50$. In addition, following backward adaptation, the majority of test stimuli (20/28, 71%, solid circles in Fig. 1) were more likely to be interpreted as walking forward. Following forward adaptation participants were more likely to interpret test stimuli as walking backward ($M = 0.60$, $SD = 0.19$) than compared with estimates of the test stimuli following control adaptation ($M = 0.65$, $SD = 0.20$),

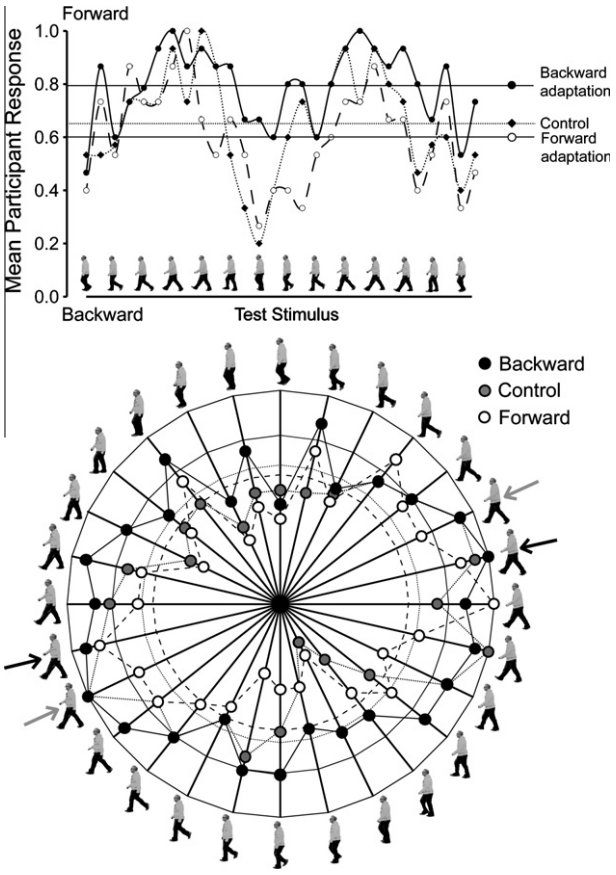

Fig. 1. Participant responses to all test stimuli following adaptation. Plotted in the upper panel are the responses to all 28 test stimuli (and mean responses: horizontal lines), following backward adaptation ($M = 0.79$, solid line), following forward adaptation ($M = 0.60$, dashed line), following Fourier phase-scrambled control adaptation ($M = 0.65$, dotted line). Alternate test stimuli are illustrated. In the lower panel the same data is illustrated as a polar plot. Responses of zero (walking backward) are at the centre of the polar plot; responses of 1 (walking forward) are at the periphery of the polar plot. Circular lines illustrate mean responses across stimuli. The black arrows indicate test stimuli most seen as walking forward following adaptation to both forward and backward walking, the grey arrows indicate the test stimuli most seen as walking forward following Fourier phase-scrambled control adaptation. All test stimuli are illustrated surrounding the polar plot.

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although this was non-significant ($F(1,14) = 1.51$, $p = 0.24$, $\eta_p^2 = 0.10$). In addition, following forward adaptation, the majority of test stimuli (17/28, 61%, open circles in Fig. 1) were more likely to be interpreted as walking backward. For almost all of the test stimuli (26/28, 93%) participants were more likely to interpret them as walking backward following forward adaptation than following backward adaptation (and vice versa).

In order to assess the degree of articulation of the test stimuli most likely to be interpreted as walking forward, we fitted smooth functions to the average responses under the three different adapting conditions (forward, backward, control). Using a non-linear minimisation of the sum of squared residuals (EzyFit toolbox, MATLAB) a Gaussian function of the following type was fitted:

$$y = a\left(\exp\left(\frac{-(x-x_0)^2}{2s^2}\right)\Big/\sqrt{(2\pi\cdot s^2)}\right) \quad (1)$$

where s represents the standard deviation of the fitted Gaussian and x_0 represents the postures most likely to be interpreted as walking forward. Gaussian functions provided a good fit to the data with all R values > 0.81. Articulated postures were most likely to be interpreted as walking forward, irrespective of the type of adapting stimulus. After adapting to forward walking ($\sigma = 5.7$, $R = 0.85$) and backward walking ($\sigma = 7.8$, $R = 0.81$), the postures most likely to be interpreted as walking forward were one frame earlier in the walking cycle than after adapting to the Fourier phase-scrambled control ($\sigma = 5.90$, $R = 0.88$). Values of x_0 are indicated by the arrows in the polar plot in Fig. 1.

In order to assess the degree of selectivity of forward walking judgements with actor posture, we calculated measures of circular variance (Mardia, 1972), a measure of the bandwidth of the participant responses when plotted in polar co-ordinates. Circular variance (V) is defined as:

$$V = 1 - \frac{|\sum_k R_k \exp(i2\theta_k)|}{\sum_k R_k} \quad (2)$$

where R_k is the participant response to the test stimulus at an angle of R_k. A circular variance of 1 shows that participants interpret all test stimuli equally indicating zero selectivity for actor posture; a value of 0 shows that participant interpretation of test stimuli were entirely dependent upon the stimulus, indicating complete selectivity for actor posture. Participant judgments after adapting to the control stimulus showed a circular variance of 0.84 indicating some selectivity to actor posture. Adapting to forward walking did not change selectivity to walker posture (circular variance = 0.84); adapting to backward walking, however, appeared to reduce selectivity to walker posture (circular variance = 0.91). A similar relationship between these measures of actor posture selectivity under the different adapting conditions is also reflected in the standard deviations of the fitted Gaussian functions (see above).

4. Experiment 2

4.1. Methods

During Experiment 2 we examined how adapting stimulus duration, and the inter-stimulus-interval (ISI) between the adapting stimulus and test stimulus, influenced the walking aftereffect within one factorial design experiment. Fourteen new participants (11 females and 3 males; mean age = 21.8 years, $SD = 4.9$ years) took part in the experiment; all participants, except the authors JI and SP, were naive to the purpose of the study. Adapting stimuli consisted of the film of the forward walking actor played either forward or backward, this film was repeated 1, 2, 4 or 8 times. The ISI was also varied: 400 ms, 800 ms or 1600 ms. Test stimuli were every alternate frame from the film of the walking actor (14 in total) in order to assess the WAE across a range of different walking postures. Test stimuli were presented once per condition (2 × adapting stimuli, 4 × adapting stimulus repeats, 3 × ISIs). All conditions occurred in a pseudorandom order.

4.2. Results

Walking aftereffects (mean responses following backward adaptation minus mean responses following forward adaptation) were calculated for each test stimulus and condition and then pooled for each adapting stimulus condition (4 durations × 3 ISIs). Fig. 2a illustrates the mean aftereffects for each adapting stimulus duration and inter-stimulus interval. Increasing the number of times the adaptation stimulus is repeated increases the adaptation aftereffect (ANOVA, main effect of adapting action repetition: $F(3,39) = 4.13$, $p < 0.05$, $\eta_p^2 = 0.24$). Furthermore, increasing the inter-stimulus interval decreases the after-effect magnitude (ANOVA, main effect of inter-stimulus interval: $F(2,26) = 4.13$, $p < 0.05$, $\eta_p^2 = 0.24$). There was no interaction between duration and inter-stimulus interval. Interestingly with one repeat of the adapting stimulus and a long inter-stimulus interval (1600 ms) the sign of the aftereffect was reversed indicating an effect similar to priming or sensitisation, where the test stimuli were interpreted as being more like the adapting stimulus, although this effect was not significant (one sample t-test: $t(13) = 1.27$, $p = 0.22$).

By separately collapsing the data across adaptation duration (Fig. 2b) and inter-stimulus interval (Fig. 2c) respectively we can better see the nature of the WAE dynamics. The build-up of the aftereffect with adapting action repeats was slightly better described by a linear function ($R^2 = 0.98$) than by a logarithmic function ($R^2 = 0.93$), although these fits will have been affected by data from one repetition of the adapting action where there was little aftereffect. The differences in the fit of these different functions, however, are too small to allow any strong conclusions to be drawn.

The duration of the WAE was dependent upon the duration of the adapting stimulus (Fig. 2d). Previous measures of this dependence have found a power-law relationship between these two factors (Hershenson, 1989, 1993; Leopold et al., 2005; Taylor, 1963), approximated by: $D = kA^x$ where D is the duration of the aftereffect, A is the adapting stimulus duration, and x is the exponent of the function. For simple MAEs the value of the exponent is near to 0.5 (a square root relationship, e.g. Hershenson, 1989); for face adaptation aftereffects estimated exponent values are higher (0.8 and 1.5, Leopold et al., 2005). In order to compare the WAE with these other aftereffects, we first calculated WAE durations by fitting linear functions for each adapting stimulus and calculating the time at which the aftereffect declined to zero. Linear functions were used as the mean aftereffect decay (Fig. 2c) was best described as a linear ($R^2 = 0.99$) rather than an exponential decay function ($R^2 = 0.92$). We then plotted the duration of the aftereffect against the duration of the adapting stimulus on log–log axes (Fig. 2d). The best fitting power function ($R^2 = 0.97$) had an exponent of 0.8, in between previous MAE and face adaptation exponent estimates.

5. Experiment 3

5.1. Methods

In Experiment 3 we examined how adapting stimulus duration and adapting stimulus walker speed influenced the magnitude of the walking aftereffect. Combinations of walker speed and stimulus duration have the same number of walking cycles; therefore it was possible to compare aftereffect magnitude when the number of walking cycles was fixed in order to test the relative influence of

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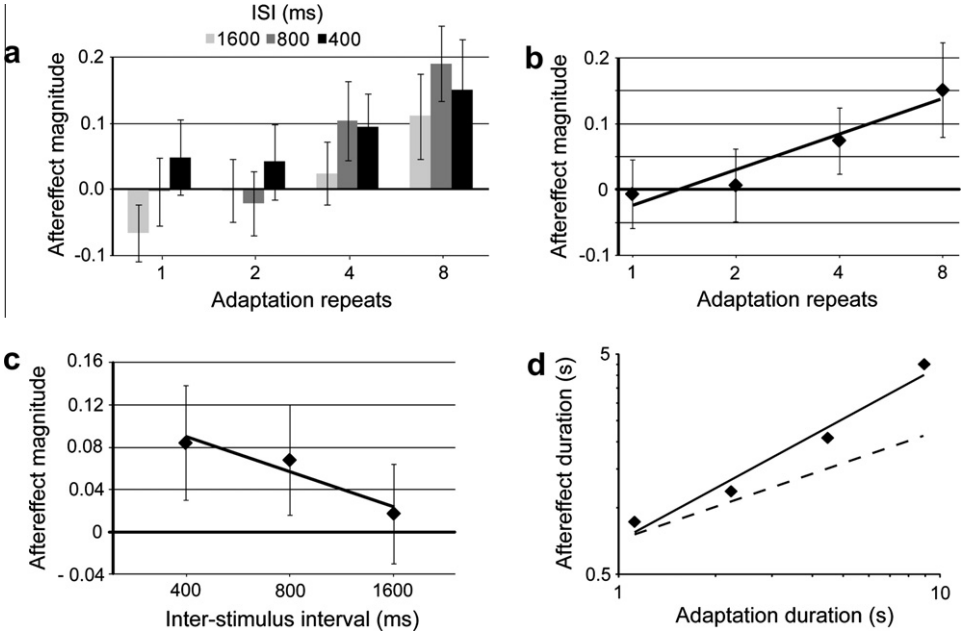

Fig. 2. Walking aftereffect dynamics. (a) Mean walking aftereffects with different repeats of the adapting action and different ISIs (in milliseconds). (b) Walking aftereffect magnitude with adapting action repeats (collapsed across ISI) plotted on a semi-log scale. (c) Walking aftereffect magnitude with ISI (collapsed across duration) plotted on a semi-log scale. (d) Aftereffect duration versus adaptation stimulus duration plotted on a log–log scale. A power law function is fitted to the data with an exponent of 0.8 (black line), the equivalent power-law function with exponent of 0.5 (dotted line) is plotted for comparison. For (a, b and c), positive values indicate that the adapting stimulus made subsequent test images appear to walk in the opposite direction. Error bars indicate SEM.

adaptation stimulus duration and adaptation stimulus walking speed.

Seventeen new participants took part in Experiment 3 (mean age = 23.9 years, *SD* = 6.1; 12 females); all participants, except the authors JI, SP and NB, were naive to the purpose of the study. The adapting stimuli were films of forward or backward walkers facing left and were played at the original (normal) speed, half speed (slow) and double speed (fast). Speed changes in walking actions were achieved by doubling the number of frames in the original movie (half speed) or removing alternate (odd) frames from the original movie (double speed). The actual speed of the limbs of the walker under the three different adapting conditions changes over time as walking actions are periodic. The most limb movement occurs when the actor appears in a standing posture as the leg moves quickly forward (or backward); the least limb movement occurs when the body is in the most articulated posture as the legs reach the limits of their swing. The average speed of leg movement (at the foot) for the normal adapting walker was 2.13 deg/s, the slow walker 1.06 deg/s and the fast walker 4.25 deg/s. We also presented adapting stimuli for different periods of time: 2240 ms (2 cycles of the original speed walker, 1 cycle of the half speed walker, 4 cycles of the double speed walker), 4480 ms and 8960 ms. The ISI between adapting and test stimulus was fixed at 400 ms. Test stimuli were every alternate frame from the film of the walking actor (14 in total) in order to assess the WAE across a range of different walking postures. Test stimuli were presented once per condition; all conditions occurred in a pseudorandom order.

5.2. Results

Walking aftereffects (mean response following backward adaptation minus mean response following forward adaptation) were calculated for each test stimulus and condition and then pooled for each adapting stimulus condition (3 speeds $\times$ 3 durations). Fig. 3a illustrates the mean strength of aftereffect as a function of both adapting stimulus duration and speed. Longer periods of adaptation resulted in larger aftereffects (ANOVA, main effect of adaptation duration: $F(2,32) = 5.47$, $p < 0.01$, $\eta_p^2 = 0.26$), and faster walkers generated larger aftereffects (ANOVA, main effect of adaptation speed: $F(2,32) = 5.18$, $p < 0.05$, $\eta_p^2 = 0.25$). There was no interaction between adaptation stimulus duration and walker speed (ANOVA, $F(4,64) = 0.61$, $p = 0.66$, $\eta_p^2 = 0.04$). Again, we observed an effect similar to priming or sensitisation with slow duration walkers repeated once, although this effect was not significant (one sample *t*-test: $t(16) = 1.20$, $p = 0.246$).

Several of the conditions had adapting stimuli containing the same number of walking cycles despite different stimulus durations and walker speeds. For example, the normal speed adapting stimulus lasting 4480 ms contained four complete walking cycles, as did the fast speed adapting stimulus lasting 2240 ms. For each pair of conditions containing the same number of walking cycles we subtracted the aftereffect from the shorter duration condition from the aftereffect from the longer duration condition. Positive values for this difference calculation indicate that the duration of the adapting stimulus has a greater effect on aftereffect magnitude than walking speed, while negative values indicate that walking speed is the dominating factor. We found that all difference calculations (5 in total) were positive, and not significantly different from each other (ANOVA: $F(2.3,35.2) = 0.24$, $p = 0.82$, $\eta_p^2 = 0.015$, Greenhouse–Geisser correction applied). This indicated that the walking aftereffect was more affected by the duration of the adapting walker than the speed at which the actor was walking, although none of these positive values were significant (one-sample *t*-tests, $t < 1.23$, $p > 0.24$).

6. General discussion

Our results replicate previous findings of a walking aftereffect (WAE) where, following prolonged exposure to a walking actor, perception of static images of actors is biased so that they are interpreted as less like the adapting stimulus (Barraclough & Jell-

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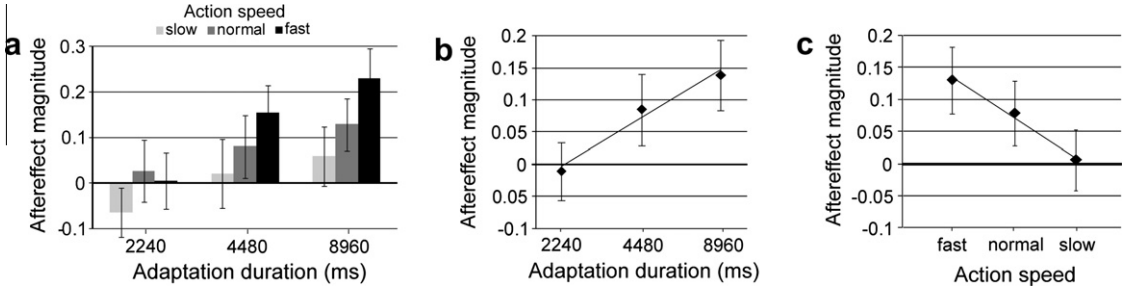

Fig. 3. Effect of adapting walker speed. (a) Mean walking aftereffects generated by walkers at different speeds observed for different durations. (b) Walking aftereffect magnitude with adapting stimulus duration (collapsed across walker speed) plotted on a semi-log scale. (c) Walking aftereffect magnitude with adapting action speed (collapsed across adapting stimulus duration). Positive values indicate that the adapting stimulus made subsequent test images appear more likely they were walking in the opposite direction. Error bars indicate SEM.

ema, 2011). After adapting to forward walking, subsequent actors are interpreted as walking backward; after adapting to backward walking, subsequent actors are interpreted as walking forward. We show here that the WAE affects static images of walkers across most actor postures. Furthermore, the WAE increases with adapting stimulus duration, decays with duration of the ISI, and is influenced by the walking speed of the adapting actor. These results indicate that the WAE follows many of the characteristic dynamics seen for face adaptation aftereffects (Leopold et al., 2005; Rhodes et al., 2007), biological motion (Troje et al., 2006), and the motion aftereffect (MAE, Hershenson, 1989, 1993). At very short adapting stimulus durations (1 repeat) and with a long duration between adapting and test stimulus or with slow walking adapting actors, test stimuli are judged as being more like the adapting stimulus, although this effect was non-significant.

When asked to interpret the direction of walking of static images of walkers in the control condition of Experiment 1, where there was effectively no adapting action, participants showed two types of biases in their estimation of the walking direction of the test stimuli: (1) a general bias towards interpreting the stimulus as walking forward and (2) a bias that appeared dependent upon the degree of articulation in the posture of the actor. An explanation for these effects can be found from single unit recordings in the monkey. In monkey Superior Temporal Sulcus (STS) separate populations of cells can be found that code selectively either forward or backward walking (e.g. Barraclough et al., 2006; Jellema & Perrett, 2006; Oram & Perrett, 1994, 1996; Vangeneugden et al., 2010). Estimates of the relative frequency of these cells suggest that approximately ¾ cells code forward walking and ¼ cells code backward walking (Oram & Perrett, 1996). Temporal lobe neurons are known to develop precise object selective tuning with visual experience (Logothetis, Pauls, & Poggio, 1995), and presumably cells coding forward and backward walking will develop as the monkeys' observe experimenters and carers walking in their close environment. The relative frequency of forward and backward walking selective cells found in monkey STS may reflect the relative frequency of the occurrence of these actions in the laboratory. We observe both forward and backward walking in our complex social environment, however, we are more likely to observe walking forward in general. The overall bias towards interpreting our test stimuli as walking forward following control adaptation is likely to reflect these lifetime experiences.

A second effect independent of the adapting stimulus was that articulated postures were often interpreted as walking forward, while standing postures, although apparently more ambiguous, tended to be interpreted as walking backward. Again, results from monkey single unit recording may provide an answer. For cells coding walking actions there is a relationship between the selectivity for the walking action and selectivity for different static images depicting walking postures (Barraclough et al., 2006). Cells that code forward walking respond significantly more to static images of walkers in articulated postures, cells that code backward walking respond significantly more to static images in standing postures. This relationship in stimulus selectivity suggests that these cells might "generalise" from static images, or brief glimpses, of walking postures to walking actions. Presented with a static image of an articulated actor, the action of walking forward is also signalled; similarly a static image of a standing actor might signal backward walking (or not walking forward). In the results of this study we show that human observers make qualitatively similar generalizations about the direction of walking movement when presented with brief glimpses of static images of walking postures.

Although there is clear variability in the magnitude of the WAE with different test stimuli (Fig. 1, and see Barraclough & Jellema, 2011), the WAE appears independent of the two biases described above. The WAE was found to affect a most images of walkers in different postures rather than influence specific stimuli. If the human visual system includes cells similar to those observed by Barraclough et al. (2006), we might expect a differential effect of forward walking adaptation on the perception of articulated postures (and an equivalent effect of backward walking adaptation on the perception of standing postures). There was a slight indication that this may be occurring following backward adaptation as several of the standing postures were increasingly interpreted as walking forward. Reflecting this, the circular variance score increased (as well as Gaussian function standard deviation) indicating the increasing bandwidth of the participant response tuning function after backward adaptation. This effect could have resulted from a reduction in the responsivity of cells coding standing postures (and backward walking) following backward adaptation. The equivalent effect, where articulated postures were less likely to be interpreted as walking forward following forward adaptation was not seen. This effect would also have appeared as a reduction in the circular variance score (and Gaussian standard deviation) after forward adaptation. A larger aftereffect following backward adaptation compared to following forward adaptation was observed, as for equivalent biological motion aftereffects (Theusner, de Lussanet, & Lappe, 2011), this may reflect a greater sensitivity to adaptation in populations of neurons coding backward walking. At this point we do not know if the human visual system contains separate populations of neurons with conjoint coding of forward walking and articulated postures and neurons with conjoint coding of backward walking and standing postures. These results suggest the conjoint coding of walking and static images is likely to be more complex than such a simple differentiation, hinted at by a recent study of monkey inferotemporal cortex and STS cell selectivity to walking action sequences and static images (Vangeneugden et al., 2011).

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The WAEs we observed here showed similar characteristic dynamics as for other visual aftereffects, including an increase with adapting stimulus repetition and decline with time; similar dynamics are seen with simple motion aftereffects (e.g. Hershenson, 1989, 1993; Taylor, 1963), aftereffects to faces (Leopold et al., 2005; Rhodes et al., 2007), gaze direction (Kloth & Schweinberger, 2008), biological motion (Troje et al., 2006) and hand actions (Barraclough et al., 2009). Our results suggest that the WAE is a measure of adaptation within visual mechanisms coding walking actions, rather than the result of other mechanisms induced by perceptual history, for example visual masking, visual object priming or other implicit memory mechanisms. Although, adaptation in low-level visual processing mechanisms is likely to be occurring simultaneously when complex walking stimuli are presented, it is unlikely to be dominating here. Previous research has ruled out an explanation for the WAE based solely upon such forms of adaptation (Barraclough & Jellema, 2011). Using the same stimuli as in this study, Barraclough and Jellema (2011) tested the effect of adapting to walking forward and backward on the perception of test stimuli facing in the same and opposite directions. Aftereffects induced in same-facing and opposite-facing test stimuli were not significantly different in magnitude, even though form and motion information were very different in the two types of stimuli. Furthermore in the above study, WAEs were seen to transfer from one actor to another with a different identity, further ruling out an explanation for the WAE based solely on low-level adaptation. Because of these previous control experiments, using the same stimuli as employed in this study, we regarded it as unnecessary to duplicate such controls here.

The shape of the decline of the WAE over time was not logarithmic as has been seen elsewhere (e.g. Leopold et al., 2005), although precisely determining this function with our restricted number of data points is difficult. Further testing of multiple inter-stimulus interval durations would be necessary to fully characterise the exact form of the WAE decay function. Similar to both the MAE (Hershenson, 1989, 1993; Taylor, 1963) and face adaptation aftereffects (Leopold et al., 2005; Rhodes et al., 2007), however, was the dependence of the duration of the aftereffect on the duration of the adapting stimulus. After a brief adapting stimulus presentation, the WAE lasted just less than a second, and ranged up to over 4 s after 8.96 s exposure to the adapting stimulus. As for both the MAE and face aftereffect, the relationship between aftereffect duration and adapting stimulus duration was well modelled by a power-law function. Our calculation of the exponent of the power-law (0.8) fell between the lower 0.5 for the MAE (Hershenson, 1989) and the higher estimates of 0.8 and 1.5 for face adaptation (Leopold et al., 2005). This intermediate value may be indicative of the relative stage of visual processing that is particularly affected by the adapting paradigm, where higher exponent values result from adaptation at later stages of visual processing. High exponents indicate that adaptation duration is less likely to saturate, indeed we demonstrate that with increasing adapting stimulus exposure, the duration of the WAE can increase dramatically.

At short adapting stimulus durations, however, we observed an effect similar to visual object priming (Tulving & Schacter, 1990) where the test stimuli were interpreted as being more like the adapting stimulus (attractive-shift). One possibility is that the different perceptual phenomena result from changes in different neural mechanisms that are sensitive to the duration of the adapting stimuli; similar effects have been observed after adapting to different duration face (Kovacs et al., 2007), and motion stimuli (Kanai & Verstraten, 2005). Kovacs et al. (2007) showed that exposure to faces for 5 s results in both position-sensitive and position-insensitive aftereffects, while exposure to faces for only 500 ms results in only a position-insensitive aftereffect, suggesting that exposure to faces for different durations results in the adaptation of separate face coding mechanisms. All face aftereffects observed, however, characteristically appeared *less* like the adapting stimuli; in this study we observe qualitatively different effects where short duration adaptation can result in an attractive effect.

Studies of the MAE may better parallel the effects we observe here. For example, Kanai and Verstraten (2005) found that after very brief (80 ms) motion adaptation a priming effect can be seen, whereas with longer duration motion adaptation (320–640 ms) an adaptation effect (repulsive-shift) is seen. They also observed an increasing "perceptual sensitisation" with time, where test stimuli increasingly appeared *more like* the adapting stimulus with a maximal effect 3 s following adaptation. Our observation of an attractive effect after a brief adapting stimulus (1 action repeat) and long inter-stimulus interval (1600 ms) could be explained by a perceptual sensitisation similar to that observed by Kanai and Verstraten. Both adaptation and perceptual sensitisation mechanisms could be acting simultaneously; after multiple repeats of the adapting stimulus and during the period immediately following, the aftereffect is dominant, however, following the decline of the aftereffect the perceptual sensitisation becomes apparent in the data.

By comparing the influence of walker speed and adapting stimulus duration (Experiment 3) we found that the WAE showed a dependence on speed similar to that observed with other MAEs. MAEs can increase with adaptor speed (e.g. Hershenson, 1989, 1993; Taylor, 1963), and under other conditions have also been shown to be well modelled by an inverted U-shaped function (e.g. Verstraten, van der Smagt, & van den Grind, 1998). The speed of our adapting walkers was relatively slow (4.25 deg/s average speed for fast walker) and the test stimuli static, and therefore are most comparable to the slow moving adapting stimuli and static test stimuli used within Verstraten, van der Smagt, and van den Grind's (1998) experiments. With stimuli moving at equivalent speeds to ours, Verstraten, van der Smagt, and van den Grind (1998) found MAE magnitudes increased with speed, i.e. on the early upward slope of the U-shaped function. It currently remains unknown whether increasing the WAE to even faster (but unrealistic) speeds would result in a subsequent decrease in WAE magnitude as would be expected if the WAE closely followed a U-shape speed tuning function.

Comparisons between the effect of increasing the adapting stimulus duration and the adapting walker speed showed that approximately equivalent increases in WAE magnitude were observed with both types of stimulus manipulation. WAE magnitude, and presumably the underlying action coding mechanism, therefore, appears to be dependent upon the number of walking cycles in the adapting stimulus, rather than on speed of the walker *per se*. With the stimuli in our experiment, it was not possible to differentiate the temporal frequency of the articulation of the walking adapting actor and the speed at which the adapting actor walked, as both simultaneously varied. Measurements of MAEs induced in static test gratings resulting from adaptation to spatial-frequency gratings, show that MAE magnitude is critically dependent upon the temporal-frequency of the adaptor rather than the adaptor speed (Pantle, 1974; Wright & Johnston, 1985). By varying the size on the screen of the walking adapting actor it may be possible to vary the speed of walking whilst maintain walking cycle frequency in order to determine the dependence of the WAE on these two factors.

6.1. Conclusions

We find that the WAE shows many characteristic dynamics previously observed in both the MAE and face adaptation aftereffects; as such the WAE appears to be a traditionally acting visual aftereffect operating at a high level in the visual system. In addition, there

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is evidence of a perceptual sensitisation following the observation of a walking actor that acts in an opposite fashion to the WAE. Our perception of human action at any one point in time appears to be a product of the characteristics of the action itself and the relative contribution of simultaneously acting mechanisms affected by our immediate perceptual experience.

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