Research Article

ASSOCIATION FOR
PSYCHOLOGICAL SCIENCE

Psychological Science
22(1) 87–94

DOI: 10.1177/0956797610391910
http://pss.sagepub.com
SAGE

Visual Aftereffects for Walking Actions Reveal Underlying Neural Mechanisms for Action Recognition

Nick Barraclough and Tjeerd Jellema
University of Hull

Abstract

The results of this study illustrate a new high-level visual aftereffect: Observing actors walking forward, without horizontal translation, makes subsequent actors appear to walk backward, and the opposite effect is obtained after observing backward walking. We used this aftereffect, which cannot be explained by simple low-level adaptation to motion direction, to investigate the properties of neural mechanisms underlying recognition of walking actions. Our results suggest that the perception of walking and the perception of static images of actors in walking postures rely on common brain mechanisms that are primarily object centered, rather than viewer centered, and that are blind to the identity of the actor. These results, obtained with human psychophysical adaptation techniques, support previous evidence accumulated using single-unit recording in nonhuman primates. In addition, these results provide evidence that current models of human action recognition require an object-centered processing stage.

Keywords

visual perception, social perception, vision, social cognition

Received 12/27/09; Revision accepted 7/30/10

In order to understand actions, humans have to be able to recognize those actions under widely varying conditions. Changes in luminance, contrast, color, size, position, angle of view, and identity of the actor typically do not influence the recognition of an action; for example, an actor walking forward will be perceived as moving in that direction irrespective of variance in these visual properties. The variation in many visual properties can, of course, influence action-detection accuracy, but this does not change the observer's understanding of the action itself. It is important that the visual system codes actions in such an invariant manner because this enables fast, accurate, and reliable interpretation of the behavior of other individuals within complex and changing social environments.

Researchers have stressed the ability of models of action coding in the visual system to explain human psychophysical results, and such models often incorporate components that mimic the physiological properties of cells recorded in monkeys (e.g., Casile & Giese, 2005; Giese & Poggio, 2003; Lange & Lappe, 2006; Schindler, Van Gool, & de Gelder, 2009; Wallis & Rolls, 1997). For example, Giese and Poggio (2003) proposed a coputational model of action recognition that takes into account several established physiological and anatomical findings. Their model includes two largely independent pathways—one that processes motion information and another that processes form information—that are analogous to the dorsal and ventral visual-processing pathways (Ungerleider & Mishkin, 1982). This model uses a feed-forward architecture, in which each subsequent level of processing incorporates feature detectors of increasing complexity; this architecture is analogous to the increasingly complex tuning of neurons in the primate visual cortical hierarchy. Although support for many component properties is provided by neuroimaging studies in humans, it is not certain whether human neurons possess the response properties of monkey neurons, on which these models are based.

Some properties of monkey cells, however, have not been incorporated in models of human action processing, despite the fact that these properties are quite well documented in monkeys. For example, cell populations in the superior temporal sulcus (STS) of the monkey code for actions in either a view-dependent or a view-independent manner. Many STS

Corresponding Author:
Nick Barraclough, Department of Psychology, University of Hull, Cottingham Rd., Hull HU6 7RX, United Kingdom
E-mail: n.barraclough@hull.ac.uk

neurons that code hand actions appear to be insensitive to the particular view of the action, but rather code the action goal (Perrett et al., 1989; Perrett, Mistlin, Harries, & Chitty, 1990). A similar coding for the action goal rather than for the action per se has been found in cells of the monkey premotor cortex, which forms part of the mirror neuron system (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001).

The monkey STS also contains neurons that are specifically sensitive to walking humans. Some of these neurons are sensitive to the specific view from which the walking action is seen (e.g., Oram & Perrett, 1994, 1996); others, however, respond when the walker is seen from any possible view (e.g., Jellema & Perrett, 2002, 2006). Although most research has concentrated on view-sensitive neurons within the monkey STS, this has perhaps been due to the usual posterior recording site in the STS, as the more anterior and largely neglected recording sites appear to have a preponderance of neurons with view-insensitive stimulus-coding properties (Jellema & Perrett, 2006). Both Giese and Poggio's (2003) and Lange and Lappe's (2006) action-processing models incorporate view-sensitive components that can explain view-sensitive human action perception (e.g., Bülthoff, Bülthoff, & Sinha, 1998). Neither of these models, however, fully reflects the object-centered, view-insensitive coding observed in cellular studies in monkeys.

It is generally agreed that monkey STS neurons that code for walking are sensitive to the compatibility of the form and motion of the action, irrespective of their view sensitivity or view insensitivity (e.g., Oram & Perrett, 1996). This sensitivity to form and motion compatibility is another property not typically incorporated in models of human action perception. Some monkey STS cells preferentially code walking in which the view and the motion direction are compatible—for example, left body-profile view and leftward body movement (forward walking). Other STS neurons are preferentially sensitive to incompatible walking—for example, left body-profile view and rightward body movement (backward walking). Sensitivity to walking compatibility in neurons that are view insensitive results in sensitivity to either forward or backward walking when that movement is seen from any angle (Jellema & Perrett, 2006). In addition, these neurons are typically insensitive to walker identity, responding equally well whoever is performing the appropriate action. Thus, given that STS cell tuning is apparently specialized for either forward or backward walking, these neurons may underlie monkeys' ability to recognize and distinguish between walking actions, irrespective of the attributes of identity and view (although, in monkeys, this ability is restricted; Vangeneugden, Vancleef, Jaeggli, VanGool, & Vogels, 2010).

A further neuronal property not accounted for in models of action perception is that many monkey STS neurons are responsive to both actions with motion and static images of actions (Barraclough, Xiao, Oram, & Perrett, 2006; Perrett, Xiao, Barraclough, Keysers, & Oram, 2009; Vangeneugden, Pollick, & Vogels, 2009). Giese and Poggio's (2003) and Lange and Lappe's (2006) models of human action recognition incorporate distinct stages, in which static images of walking individuals are processed before integration at a higher level of processing in order to code the moving action. These models have received support from human neuroimaging studies that suggest that separate cortical areas are differentially sensitive to static and to moving images of acting humans (e.g., Downing, Peelen, Wiggett, & Tew, 2006). However, there is recent support for the notion that the human brain jointly processes static images of actors and actions with motion (e.g., Lorteije et al., 2007).

In summary, when it comes to representing actions, monkey STS cell responsiveness can be quite specific. Some cells are selectively responsive to either one or several specific views (view sensitive), and other cells are sensitive to each and every view (object-centered coding). Further, some cells are sensitive to the compatibility (or incompatibility) of form and motion (forward walking as opposed to backward walking). However, in contrast to this specificity, the cells tend to respond to both real actions and static images related to those actions. It is not certain whether there are populations of neurons in the human brain with similar coding properties.

Although it is not feasible to test directly whether human neurons underlying walking recognition show response properties similar to those observed in monkeys, it is possible to test this indirectly using psychophysical adaptation techniques. Adaptation has often been referred to as the "psychophysicist's electrode" because of its power to temporarily reduce the sensitivity of discrete neuronal populations tuned to the adapting stimulus. Subsequently induced perceptual aftereffects can be used to infer properties of the neural mechanisms underlying the perception of the adapting and other tested stimuli. Adaptation paradigms have been widely used to elucidate the neural underpinnings of the perception and recognition of complex biological objects in the area of face perception (Leopold, O'Toole, Vetter, & Blanz, 2001; Webster, Kaping, Mizokami, & Duhamel, 2004); these paradigms use static adapting images as well as dynamic biological actions (Barraclough, Keith, Xiao, Oram, & Perrett, 2009). In the current study, we used adaptation techniques to determine the sensitivity of those neural mechanisms that underlie the recognition of forward and backward walking in humans.

We first tested whether observation of a film of an actor walking forward (or backward) induced a bias in the perception of subsequent movies and static images of a walking actor (Experiment 1). Having established that such observation did generate an aftereffect, we performed two further experiments to investigate the mechanisms underlying the recognition of walking actions. We tested whether walking recognition in humans relies on viewer-centered or object-centered mechanisms (Experiment 2) and whether walking recognition mechanisms are sensitive to actor identity (Experiment 3).

General Method

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 and were naive to the purpose of the experiments. Experiments were approved by the ethics committee of the Department of Psychology, University of Hull.

Stimuli

Two actors (Actor 1 was male; Actor 2 was female) were filmed walking forward to the left and backward to the left, at angles 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 30 frames (duration = 1,200 ms; i.e., 40 ms/frame). In each frame, the background was colored midgray, and the actor's entire body was centered 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 or backward walking) to the articulatory movements of the actor rather than allowing a simple comparison between body translation and body view.

These four films (two actors, each moving forward and backward) were used to generate all stimuli. Films were flipped from left to right to generate a different view of the actor. Each film showed one walking cycle.

Experimental procedure

A computer running MATLAB 2006a (The MathWorks, Natick, MA) and the Cogent Graphics toolbox (Laboratory of Neurobiology, University College London, England) was used to control experiments, display stimuli (22.3° × 16.6° of visual angle) on a 22-in. flat-screen CRT monitor (Philips 202P40; 1,600 × 1,200 pixels, 100-Hz refresh rate), and record participants' responses.

All experiments followed the same procedure. First, in the preadaptation test phase, participants were told that they would be shown static images (duration = 80 ms) or very short movies consisting of two frames (total duration = 80 ms), all of which were taken from a film of an actor walking either forward or backward. Pairs of frames (see Fig. 1) shown in immediate succession were expected to result in a strong perception of biological motion consistent with the normal movements of the human body (Chatterjee, Freyd, & Shiffrar, 1996). On each trial, participants indicated on the computer keyboard whether the actor was walking forward or backward. After the participant made his or her response, the screen remained blank (gray) for 1,500 ms before the start of the next trial. Test stimuli were presented in pseudorandom order.

Next, the participant took part in the adaptation phase of the experiment, in which experimental methods were the same as in the preadaptation phase, except that on every trial an adapting stimulus (four repeats of a film; total duration = 4,800 ms) was presented first, followed by a short (150 ms) interstimulus interval and then a test stimulus. Participants participated in two sessions on separate days (maximum separation = 7 days); in each session, adaptation to a different walking direction was tested (e.g., if participants initially saw a film depicting forward walking, they were shown a film depicting backward walking on the subsequent day). The order of adapting phases was counterbalanced so that a random selection of half the participants (or approximately half when there was an odd numbers of participants) adapted to forward walking first.

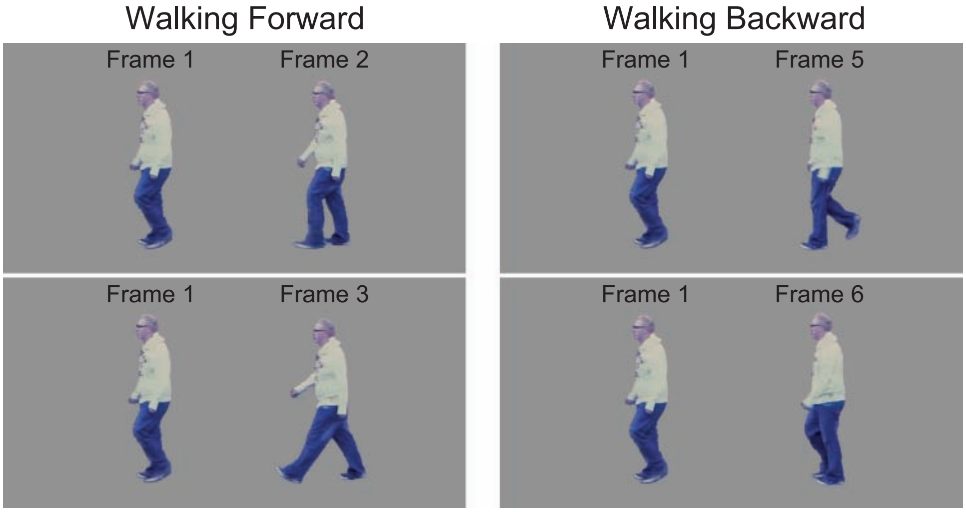

Fig. 1. Pairs of static images of Actor 1 used as test stimuli. When two of these images are shown in rapid succession (e.g., Frame 1 followed by Frame 5 of the same film), the actor appears to walk. The example pairs on the left are typically seen as showing the actor walking forward, and the example pairs on the right are typically seen as showing the actor walking backward.

For each participant, the mean rating of each test stimulus in the preadaptation phase was subtracted from the mean rating of the same test stimulus from the adaptation phase to calculate the action aftereffect. Because all subjects participated in two sessions in the adaptation phase (adaptation to forward and backward walking), there were two measures of the action aftereffect: a forward aftereffect and a backward aftereffect. Positive aftereffect values indicated that adaptation biased perception so that test stimuli were more likely to be perceived as walking forward; negative aftereffect values indicated that test stimuli were more likely to be perceived as walking backward.

Experiment 1: Can Observation of Walking Generate Aftereffects?

Method

Experiment 1 tested whether there was an aftereffect for observing forward and backward walking actions. We also tested whether adaptation influenced the perception of (a) short two-frame movies of walking actors and (b) static images of actors in walking postures. Our rationale was that if adaptation to walking biases the perception of walking actions and static images in a similar manner, then the perception of these two stimulus types relies on common underlying brain mechanisms.

Sixteen participants (8 females and 8 males; mean age = 20.6 years, *SD* = 0.5 years) took part in Experiment 1. Adapting stimuli consisted of films of Actor 1 walking forward or backward while facing left. Test stimuli consisted of five test movies and five test images of Actor 1 facing left; these movies and images were taken from the same film as the adapting stimuli were, but the frame sequences in each case were different. Each test stimulus was shown 10 times.

Results and discussion

Participants' ratings of test stimuli (see Fig. 2a) were significantly different under different conditions. An analysis of variance (ANOVA) with factors of adaptation (preadaptation, after forward adaptation, or after backward adaptation) revealed a main effect of adaptation, $F(1.4, 21.3) = 13.43$, $p < .001$, $\eta_p^2 = .47$, Greenhouse-Geisser correction applied. Planned contrasts indicated that after adapting to a movie of an actor walking forward, participants were significantly more likely to rate test stimuli as walking backward—preadaptation compared with forward adaptation, $F(1, 15) = 5.24$, $p < .05$, $\eta_p^2 = .26$ (see Fig. 2a). After adapting to movies of an actor walking backward, participants were significantly more likely to rate test stimuli as walking forward—preadaptation compared with backward adaptation, $F(1, 15) = 17.59$, $p < .001$, $\eta_p^2 = .54$ (see Fig. 2a).

Having established that there is a robust aftereffect from observing both forward and backward walking in a range of test stimuli (see Fig. 2b), we pooled the mean aftereffects (across stimulus exemplars) for the two test-stimulus conditions (movies and images; see Fig. 2c). We examined the effect of test-stimulus condition in an ANOVA (while inverting the

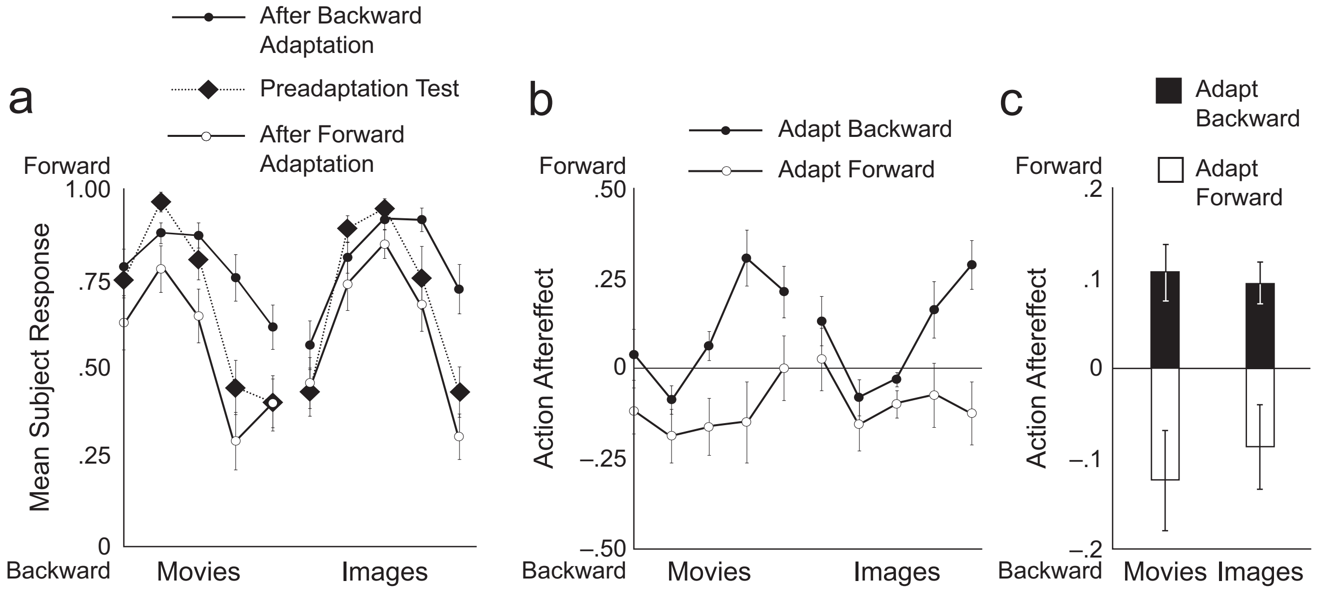

Fig. 2. Action adaptation aftereffect in Experiment 1. The graph in (a) plots the mean response to each test stimulus (five movies and five pairs of static images) before adaptation, after adaptation to an actor walking forward, and after adaptation to an actor walking backward; a value of 1 indicates that participants always perceived the test stimulus as walking forward, and a value of 0 indicates that the stimulus was always perceived as walking backward. The mean action aftereffect was calculated for each test stimulus and for each adaptation condition by subtracting the mean response before adaptation from the mean response after adaptation (b). The bar graph (c) shows these mean aftereffects pooled across stimuli. In (b) and (c), positive or negative values indicate whether the test stimulus was more likely to be seen as walking forward or backward, respectively. Error bars indicate standard errors of the mean.

sign of the backward aftereffect; cf. Barraclough et al., 2009). There was no significant main effect of test-stimulus condition, $F(1, 15) = 0.16$, $p = .70$, $\eta_p^2 = .01$, nor was there an interaction between test-stimulus condition and adapting stimulus, $F(1, 15) = 1.70$, $p = .21$, $\eta_p^2 = .10$. These results indicate that the perception of walking and the perception of static images of walkers are similarly affected by adaptation to moving walkers.

Experiment 2: Are Walking Aftereffects Dependent on View?

Method

Having established that a walking aftereffect biased the perception of both movies and static images of walking, we next examined whether the action aftereffect could be found in test actors seen from a view different from the view of the adapting actor. We hypothesized that if walking aftereffects were generated regardless of whether stimuli were seen from the same viewpoint as the adapting stimulus, then the neural mechanisms underlying the perception of walking compatibility (forward or backward) must be object centered.

Nineteen new participants (15 females and 4 males; mean age = 28.9 years, *SD* = 7.4 years) took part in Experiment 2. The adapting stimuli were films of forward and backward walking facing left (for 8 female and 2 male participants) and films of forward and backing walking facing right (for 7 female and 2 male participants). Test stimuli (five movies and five images) different from those used in Experiment 1 were taken from the film of Actor 1 walking forward facing left, and a duplicate set of these stimuli were flipped horizontally so that the actor faced right. There were thus 20 test stimuli in total: 10 movies and 10 images. Half of each group of stimuli showed the actor facing in the same direction as the actor in the adapting stimulus, and half showed the actor facing in the opposite direction; each test stimulus was shown 10 times.

Results and discussion

Forward and backward walking aftereffects were calculated for each of the 20 test stimuli, then pooled for the four different conditions (test-stimulus type: movies or images; test-stimulus view: same or opposite; see Fig. 3). There was a significant difference between the forward and backward walking aftereffects: An ANOVA yielded a main effect for adapting stimulus, $F(1, 18) = 13.14$, $p < .005$, $\eta_p^2 = .42$. We also tested the effect of the test-stimulus conditions in an ANOVA (while inverting the sign of the backward aftereffect); there were no significant main effects of test-stimulus type, test-stimulus view, or adapting stimulus and no significant interactions. Performing a four-way mixed ANOVA to assess the additional, between-subjects factor of the direction that the actor in the adapting stimulus faced (left or right) did not result in any significant main effects or interactions. These results indicate that test-stimulus view and test-stimulus type did not have a significant effect on aftereffect magnitude. In the final experiment, we tested whether these mechanisms underlying the perception of walking are sensitive to actor identity.

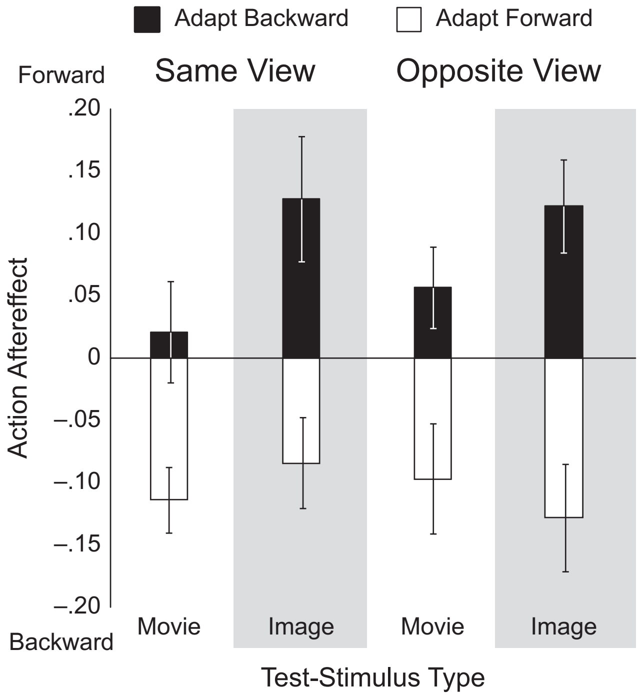

Fig. 3. Aftereffects in Experiment 2 as a function of test-stimulus type (movie or static image) and test-stimulus view (same view or opposite view relative to the adapting stimulus). Results are shown for test stimuli following adaptation to forward walking and adaptation to backward walking. Positive or negative values indicate whether the actor was more likely to be perceived as walking forward or backward, respectively. Error bars indicate standard errors of the mean.

Experiment 3: Are Walking Aftereffects Dependent on Identity?

Method

The previous two experiments demonstrated that the perception of walking and the perception of static images of walkers rely on a common brain mechanism that is insensitive to the view from which the actor is observed. Experiment 3 tested whether this mechanism is sensitive to the actor's identity. We made the assumption that the degree of sensitivity to actor identity would be similar whether the test stimulus was moving or not, and so we tested identity sensitivity with test movies only. We hypothesized that if the walking aftereffects generated were the same regardless of whether the adapting and test stimuli showed the same actor or different actors, then the neural mechanisms underlying the perception of walking are insensitive to identity.

Fifteen new participants (5 females and 10 males; mean age = 31.1 years, *SD* = 7.9 years) took part in Experiment 3.

The adapting stimuli were the films of forward and backward walking of either Actor 1 (for 2 female and 5 male participants) or Actor 2 (for 3 female and 5 male participants; Actor 1 and Actor 2 differed in sex, race, and clothing). The test movies selected for Actor 1 were different from those used in Experiments 1 and 2. There were 48 movies per actor shown once each; all participants saw all test movies.

Results

Forward and backward walking aftereffects were calculated for each of the test stimuli and then pooled for the two different test-stimulus conditions (same identity or different identity; see Fig. 4). As in Experiments 1 and 2, there was a significant difference between the forward and backward walking aftereffects; an ANOVA yielded a main effect for adapting stimulus, $F(1, 14) = 12.61$, $p < .005$, $\eta_p^2 = .47$. We also tested the effect of actor identity in an ANOVA (while inverting the sign of the backward aftereffect); there was no significant main effect of identity nor an interaction between identity and adapting stimulus. Thus, adaptation aftereffects induced by the same actor and by different actors were not significantly different.

General Discussion

Our results provide important information about the neural mechanisms underlying action recognition by demonstrating that adaptation to walking affects the subsequent perception of both walking and static images of walkers. In addition, this perception transfers to walkers seen from different views and to different walkers. Changes in luminance, contrast, color, size, position, angle of view, and identity of the actor typically do not influence action recognition; our studies, however, show that the immediate perceptual history of the action does influence action recognition. We did not choose to measure the dynamics of the reported aftereffect induced by the immediate perceptual history (e.g., how the aftereffect builds up as the duration of the adapting stimulus increases, how long the aftereffect lasts), but rather we used the aftereffect to investigate some of the properties of the brain mechanisms underlying the perception of walkers (cf. Jordan, Fallah, & Stoner, 2006). We expect that the dynamics of this aftereffect are similar to the dynamics of other high-level aftereffects, such as those observed in faces, biological motion, and hand actions (e.g., Barraclough et al., 2009; Leopold, Rhodes, Muller, & Jeffery, 2005; Troje, Sadr, Geyer, & Nakayama, 2006), in which adaptation magnitude increases as the duration of the adapting stimulus increases and decreases as the interstimulus interval and test-stimulus duration increase.

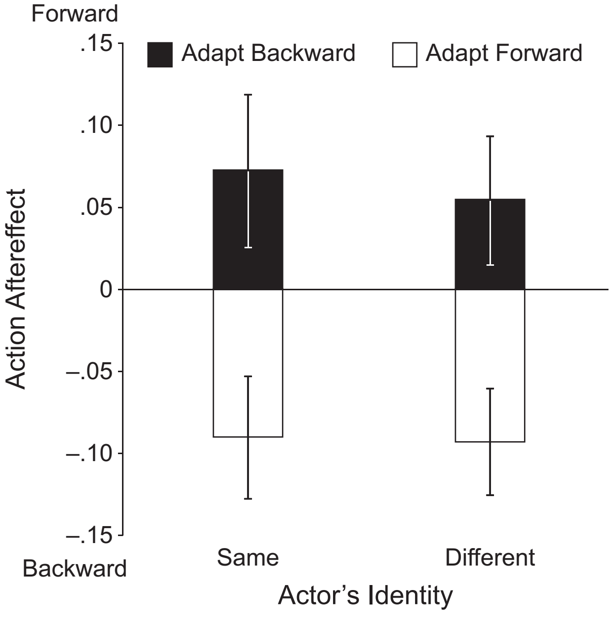

Fig. 4. Aftereffects in Experiment 3 as a function of the actor's identity (same or different relative to the adapting stimulus). Results are shown for test stimuli following adaptation to forward walking and adaptation to backward walking. Positive or negative values indicate whether the actor was more likely to be perceived as walking forward or backward, respectively. Error bars indicate standard errors of the mean.

Common coding of motion and static images depicting motion

The biases in the percepts of both the moving test walkers and the static images of test walkers, which make the walkers appear to be moving in the direction opposite the direction in which they are actually moving, suggest that in humans there are separate populations of neurons coding forward and backward walking. In addition, these putative neurons appear to act in an opponent fashion, similar to the behavior of monkey neurons (cf. Barraclough et al., 2006; Oram & Perrett, 1996). Furthermore, the results suggest that putative populations of neurons coding static images of walkers (cf. Barraclough et al., 2006) are also affected by adaptation to walking and are sensitive to walking compatibility, and this indicates a potential common coding of moving and static walkers. Similar generalized coding of walking actions in monkey STS neurons was observed by Barraclough et al. (2006), who argued that such generalizing may allow these neurons to code actions when limited visual information is available, for example, during a brief glimpse and in the absence of motion information. This interpretation of our results is at odds with studies that suggest that separate brain mechanisms process static images of human postures depicting an action and real human walking (e.g., Downing et al., 2006). This interpretation also contradicts the assumptions of models of human action perception that propose separate processing of body form and actions (Giese & Poggio, 2003; Lange & Lappe, 2006). Our results, however, are in line with the findings of several studies that have suggested that the neural substrates for real and implied biological motion may overlap considerably (Kourtzi & Kanwisher, 2000; Lorteije et al., 2006, 2007; Senior et al., 2000).

Viewpoint dependence

Our results showing that test-stimulus view did not have a significant effect on aftereffect magnitude suggest that the neural mechanisms underlying walking recognition are insensitive to the view from which the actor is observed. This finding of view insensitivity is reminiscent of findings suggesting that view-insensitive neurons code walking in the monkey STS (Jellema & Perrett, 2006). Other studies using visual adaptation techniques and stimuli related to the ones we used in this study have also typically found that coding can be view independent; such stimuli include hand actions (Barraclough et al., 2009), facial expressions (Benton et al., 2007), and biological motion (Grossman, Jardine, & Pyles, 2010). Indeed, all these stimuli are coded by neural mechanisms located within the STS, and view independence may be a characteristic of STS adaptation.

One interpretation of our findings is that the aftereffects we observed could be the result of adaptation at a low level in the visual system. We do not rule out aftereffects at these low levels or indeed within areas that code actions in a view-dependent manner (e.g., the extrastriate body area; Chan, Peelen, & Downing, 2004). These aftereffects, however, are unlikely to dominate, as they cannot explain the view-independent aftereffects we observed. The low-level characteristics (e.g., form and motion) of the adapting and test stimuli were very different. Indeed, local motion vectors were effectively reversed in direction when viewpoint invariance was tested. If low-level motion adaptation was the dominating influence, the sign of the forward and backward aftereffects would be reversed; as this was not the case, these experiments provide a control for the influence of adaptation in low-level motion detectors.

Although Giese and Poggio's (2003) action-perception model stresses view-sensitive coding of actions in order to explain some psychophysical results (e.g., Bülthoff et al., 1998; Chan et al., 2004), this model is based on previous hierarchical models of object perception that include a later view-independent stage (Riesenhuber & Poggio, 1999, 2002). Our results indicate that a view-independent stage of processing should be incorporated into action-processing models.

The identity independence we observed lends support to the identity independence modeled by both Giese and Poggio (2003) and Lange and Lappe (2006). Monkey STS neurons coding walking compatibility in a view-invariant way (Jellema & Perrett, 2006) are also insensitive to identity, and activity in similar neuronal populations in humans may underlie the results we observed in our experiments.

We have shown that observing humans walking generates aftereffects that bias the subsequent perception of walking. This adaptation phenomenon allowed us to investigate the brain mechanisms underlying these perceptual processes. We found that when observers are judging whether an actor is walking forward or backward, they use view- and identity-insensitive neural mechanisms that generalize across moving and static actors (with implied motion). Adaptation in neuronal populations with response properties similar to those observed in the monkey anterior STS may underpin our results, and this suggests that neurons with similar coding properties exist in the human visual system.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was funded by the British Academy.

References

Barraclough, N.E., Keith, R.H., Xiao, D.-K., Oram, M.W., & Perrett, D.I. (2009). Visual adaptation to goal-directed hand actions. *Journal of Cognitive Neuroscience*, *21*, 1806–1820.

Barraclough, N.E., Xiao, D.-K., Oram, M.W., & Perrett, D.I. (2006). The sensitivity of primate STS neurons to walking sequences and to the degree of articulation in static images. *Progress in Brain Research*, *154*, 135–148.

Benton, C.P., Etchells, P.J., Porter, G., Clark, A.P., Penton-Voak, I.S., & Nikolov, S.G. (2007). Turning the other cheek: The viewpoint dependence of facial expression after-effects. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 2131–2137.

Bülthoff, I., Bülthoff, H., & Sinha, P. (1998). Top-down influences on stereoscopic depth-perception. *Nature Neuroscience*, *1*, 254–257.

Casile, A., & Giese, M.A. (2005). Critical features for the recognition of biological motion. *Journal of Vision*, *5*(4), Article 6. Retrieved December 9, 2008, from http://www.journalofvision.org/content/5/4/6

Chan, A.W.Y., Peelen, M.V., & Downing, P.E. (2004). The effect of viewpoint on body representation in the extrastriate body area. *NeuroReport*, *15*, 2407–2410.

Chatterjee, S.H., Freyd, J.J., & Shiffrar, M. (1996). Configural processing in the perception of apparent biological motion. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 916–929.

Downing, P.E., Peelen, M.V., Wiggett, A.J., & Tew, B.D. (2006). The role of the extrastriate body area in action perception. *Social Neuroscience*, *1*, 52–62.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Giese, M.A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*, 179–192.

Grossman, E.D., Jardine, N.L., & Pyles, J.A. (2010). fMR-adaptation reveals invariant coding of biological motion on the human STS. *Frontiers in Human Neuroscience*, *4*, 1–18.

Jellema, T., & Perrett, D.I. (2002). Coding of visible and hidden actions. In W. Prinz & B. Hommel (Eds.), *Attention and performance XIX: Common mechanisms in perception and action* (pp. 356–380). New York, NY: Oxford University Press.

Jellema, T., & Perrett, D.I. (2006). Neural representations of perceived bodily actions using a categorical frame of reference. *Neuropsychologia*, *44*, 1535–1546.

Jordan, H., Fallah, M., & Stoner, G.R. (2006). Adaptation of gender derived from biological motion. *Nature Neuroscience*, *9*, 738–739.

Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, *12*, 48–55.

Lange, J., & Lappe, M. (2006). A model of biological motion perception from configural form cues. *Journal of Neuroscience*, *26*, 2894–2906.

Leopold, D.A., O'Toole, A.J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, *4*, 89–94.

Leopold, D.A., Rhodes, G., Muller, K.-M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 897–904.

Lorteije, J.A.M., Kenemans, J.L., Jellema, T., van der Lubbe, R.H.J., de Heer, F., & van Wezel, R.J.A. (2006). Delayed response to animate implied motion in human motion processing areas. *Journal of Cognitive Neuroscience*, *18*, 1–11.

Lorteije, J.A.M., Kenemans, J.L., Jellema, T., van der Lubbe, R.H.J., Lommers, M.W., & van Wezel, R.J.A. (2007). Adaptation to real motion reveals direction selective interactions between real and implied motion processing. *Journal of Cognitive Neuroscience*, *19*, 1231–1240.

Oram, M.W., & Perrett, D.I. (1994). Responses of anterior superior temporal polysensory (STPa) neurons to "biological motion" stimuli. *Journal of Cognitive Neuroscience*, *6*, 99–116.

Oram, M.W., & Perrett, D.I. (1996). Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the macaque monkey. *Journal of Neurophysiology*, *76*, 109–129.

Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., et al. (1989). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology*, *146*, 87–113.

Perrett, D.I., Mistlin, A.J., Harries, M.H., & Chitty, A.J. (1990). Understanding the visual appearance and consequences of hand actions. In M.A. Goodale (Ed.), *Vision and action: The control of action* (pp. 163–180). Norwood, NJ: Ablex.

Perrett, D.I., Xiao, D.-K., Barraclough, N.E., Keysers, C., & Oram, M.W. (2009). Seeing the future: Natural image sequences produce "anticipatory" neuronal activity and bias perceptual report. *Quarterly Journal of Experimental Psychology*, *62*, 2081–2104.

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, *2*, 1019–1025.

Riesenhuber, M., & Poggio, T. (2002). Neural mechanisms of object recognition. *Current Opinion in Neurobiology*, *12*, 162–168.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661–670.

Schindler, K., Van Gool, L., & de Gelder, B. (2009). Recognizing emotions expressed by body pose: A biologically inspired neural model. *Neural Networks*, *21*, 1238–1246.

Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E.T., Brammer, M., & David, A.S. (2000). The functional neuroanatomy of implicit-motion perception or representational momentum. *Current Biology*, *10*, 16–22.

Troje, N.F., Sadr, J., Geyer, H., & Nakayama, K. (2006). Adaptation aftereffects in the perception of gender from biological motion. *Journal of Vision*, *6*(8), Article 7. Retrieved December 4, 2007, from http://www.journalofvision.org/content/6/8/7

Ungerleider, L.G., & Mishkin, M. (1982). Two cortical visual systems. In J. Ingle, M.A. Goodale, & R.J.W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

Vangeneugden, J., Pollick, F., & Vogels, R. (2009). Functional differentiation of macaque visual temporal cortical neurons using a parametric action space. *Cerebral Cortex*, *19*, 593–611.

Vangeneugden, J., Vancleef, K., Jaeggli, T., VanGool, L., & Vogels, R. (2010). Discrimination of locomotion direction in impoverished displays of walkers by macaque monkeys. *Journal of Vision*, *10*(4), Article 22. Retrieved July 20, 2010, from http://www.journalofvision.org/content/10/4/22

Wallis, G., & Rolls, E.T. (1997). Invariant face and object recognition in the visual system. *Progress in Neurobiology*, *51*, 167–194.

Webster, M.A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*, 557–561.