ᡅᠠᡗ

850

Adaptation aftereffects in the perception of gender from biological motion

Nikolaus F. Troje

Javid Sadr

Henning Geyer

Ken Nakayama

Department of Psychology, Queen's University, Kingston, Ontario, Canada, & Ruhr-University, Bochum, Germany Department of Psychology, Harvard University, Boston, MA, USA Department of Psychology, Ruhr-University,

Bochum, Germany

Department of Psychology, Harvard University, Boston, MA, USA

Human visual perception is highly adaptive. While this has been known and studied for a long time in domains such as color vision, motion perception, or the processing of spatial frequency, a number of more recent studies have shown that adaptation and adaptation aftereffects also occur in high-level visual domains like shape perception and face recognition. Here, we present data that demonstrate a pronounced aftereffect in response to adaptation to the perceived gender of biological motion point-light walkers. A walker that is perceived to be ambiguous in gender under neutral adaptation appears to be male after adaptation with an exaggerated female walker and female after adaptation with an exaggerated male walker. We discuss this adaptation aftereffect as a tool to characterize and probe the mechanisms underlying biological motion perception.

Keywords: biological motion, adaptation, aftereffect, sex classification

Introduction

The compelling and perceptually rich nature of biological motion, as exemplified by human movement represented only by point lights at a few joints, has received a great deal of attention following the pioneering work of Johansson (1973, 1975). Since that time, a wide variety of research has investigated our ability to perceive important characteristics of both actors and their actions, along with the various factors that influence underlying perceptual processes. One aspect of biological motion perception that has been studied in some detail in recent decades has been our ability to discriminate the gender of individuals represented as point-light actors (e.g., point-light walkers). Not long after Johansson's first reports, Kozlowski & Cutting (1977, 1978) investigated participants' accuracy in gender discriminations of point-light walkers in video (viewed from the side), along with the influence of arm swing, walking speed, and partial occlusion on this discriminative ability. Barclay, Cutting, & Kozlowski (1978) further studied the influence of exposure duration, video speed, blurring, and inversion. Subsequently, work by Runeson and Frykholm (1983) sought to quantify the accuracy of gender discrimination during complex activity, including walking, sitting, jumping, lifting, and so forth, and even explored the subtle but significant

distinction between perceiving veridical versus feigned, acted gender. Mather and Murdoch (1994) explicitly explored the relative contributions of the shoulder-hip ratio as an example for a static cue and lateral body sway as an example for a dynamic cue in gender perception. In pitting one against the other, they observed that the influence of the chosen dynamic cue on gender discrimination seemed to outweigh that of the static cue. These researchers also tested participants with frontal-view point-light walkers presented very briefly (i.e., fractions of a walk cycle), showing accurate gender perception at even these short exposures. Troje (2002a) extended these findings by showing that, for gender classification, dynamic information is generally more informative than static cues contained in point-light displays of human walkers.

Quite independent of this work on gender perception, it has been shown that biological motion perception is modulated by factors such as perceptual priming, nonfocal task-irrelevant stimulus processing, and even concurrent motor activity on participants' processing of biological motion stimuli (Jacobs & Shiffrar, 2005; Nilsson, Olofsson, & Nyberg, 1992; Olofsson, Nyberg, & Nilsson, 1997; Thornton & Vuong, 2004; Verfaillie, 2000).

Here, our interest is in extending the existing work on gender perception in biological motion by exploring its manipulation by "extraneous" stimuli and perceptual history. Particularly, we assess whether and to what extent gender discrimination of a point-light walker can be biased by exposure to a preceding biological motion display. Such an effect might be analogous to other adaptation aftereffects observed in both low- and high-level visual domains. Adaptation aftereffects have played an important role in shaping the understanding of basic visual dimensions such as color, motion, spatial frequency, and orientation (e.g., see reviews by Clifford, Wenderoth, & Spehar, 2000; Wade & Verstraten, 1998; Webster, 1996). However, they are not restricted to low-level visual processing. Over the past few years, it has become obvious that even complex processes such as face perception are subject to intriguing aftereffects, which may shed light on underlying mechanisms and representations. An adaptation effect for face shape (i.e., a figural aftereffect due to a face-distortion manipulation) was described by Webster and MacLin (1999), and the generalization of this effect over image size and orientation, including inversion, was further assessed by Watson and Clifford (2003) and Zhao and Chubb (2001), respectively. Rhodes, Jeffery, Watson, Clifford, and Nakayama (2003) showed similar aftereffects for judgments of facial attractiveness, and these adaptation effects have also been seen in the perception of facial categories such as gender, ethnicity, and expression (Hsu & Young, 2004; Webster, Kaping, Mizokami, & Duhamel, 2004). Perhaps more surprisingly, an adaptation effect has also been shown in the perception of facial identity: Leopold, O'Toole, Vetter, and Blanz (2001) derived "antifaces" from face stimuli by subtracting the differences between an individual face and an average, prototypical face from the prototype and showed that adaptation with such an antiface resulted in a pronounced aftereffect. Observers now perceived the previously neutral prototype as resembling the face from which the antiface was derived. Interestingly, the dynamics of the buildup and decay of the adaptation effect show characteristics that are very similar to the ones observed for lowlevel visual aftereffects (Leopold, Rhodes, Müller, & Jeffrey, 2005). On the other hand, it has been demonstrated that the face identity aftereffect is, to a large degree, invariant to position, scale, and orientation of the faces, which implies that it is unlikely to simply derive from cumulative adaptation of low-level features (Rhodes et al., 2003; Watson & Clifford, 2003; Zhao & Chubb, 2001).

The basis of the work by Leopold et al. (2001) is a system that allows faces to be treated as objects in a linear, morphable space (Blanz & Vetter, 1999; Vetter & Troje, 1997). A similar system developed by Troje (2002a, 2002b) allows us to represent and manipulate biological motion stimuli in a linear framework. This approach maps individual biological motion point-light walkers into a metric, morphable space wherein we can measure distances between individual walkers, generate synthetic "average" walkers and other linear combinations of existing walkers, and derive linear classifiers from

In the current experiments, we used this approach to generate perceptually neutral and exaggerated male and female point-light walkers for use as adapting stimuli as well as to systematically sample a range of walkers along the gender axis for probing the participants' responses to a parametric, well-defined set of test stimuli. In preliminary experiments (Troje & Geyer, 2002), we had observed a prominent shift in the perceived gender of a walker after presentation of a previously shown caricature of a male or a female walker. A neutral walker was perceived to be female after adaptation with the exaggerated male walker, and it was perceived to be male after adaptation with the exaggerated female walker. The purpose of the current study is to demonstrate and document this pronounced aftereffect and to investigate its dependence on the duration of exposure to the adapting and test stimuli and on the duration of the storage period in between. Perceptual aftereffects usually show an increase with the duration of the adapting stimulus and a decrease with both the storage time and the duration of the test stimulus (e.g., Hershenson, 1989), which is not generally expected for simple priming effects.

Methods

Participants

Eighteen participants took part in the first part of this study wherein we measured a baseline for the following adaptation experiments. Half of them were male and half were female. Their mean age was 26.6 years (*SD*, 5.1 years). Twelve of them stayed with us for the adaptation experiments (6 males and 6 females; age, 27.7 ± 5.2 years). All of them were students at the Department of Psychology of Ruhr-University, and they received course credit for their participation. Experiments were in compliance with the local human subjects guidelines and approved by the Human Ethics Committee of Ruhr-University.

Stimuli

The point-light walkers used as stimuli in this study were generated using a technique described in detail by Troje (2002a, 2002b). Briefly stated here, 20 male and 20 female walkers were attached with an array of 38 retroreflective markers whose three-dimensional trajectories were recorded with a 9-camera motion capture system (Vicon 512, Oxford Metrics) at a sampling rate of 120 Hz. Based on the marker trajectories, a biomechanical model (BodyBuilder, Oxford Metrics) was applied to compute the locations of 12 major joints, as well as the centers of pelvis, thorax, and head.

Following Troje (2002b), the data were then subjected to a discrete Fourier decomposition, resulting in a parametric, morphable representation of each original walker as a 226-dimensional vector describing both static and dynamic information for each of the 15 locations. Represented in this way and given each walker's known gender, discriminant function analysis was performed to create an axis that reflects the differences between male and female walkers in terms of a linear classifier. The resulting axis was then scaled in *z* scores with respect to the distribution of the 40 walkers. Position 0 indicates the average walker. Position +1 corresponds to a walker 1 standard deviation (*SD*) away from the mean into the male part of the space, and a position of -1 refers to a walker 1 *SD* away from the mean into the female part of the space.

In the baseline study (no adaptation, variable exposure duration), participants' male/female responses were measured for 13 walkers sampled at equidistant intervals between -3.5 SD (female) and +3.5 SD (male) along this axis. On the basis of the results of this baseline study, we chose the adaptation stimuli used in the three types of adaptation tests (variable test, storage, and adaptation times; see below) as follows: A perceptually genderneutral walker was generated at -1 SD (somewhat more female than the mathematical average), an exaggerated female walker was generated at -7 SD, and an exaggerated male walker was generated at +5 SD. After adaptation, participants were probed with walkers generated at seven equidistant steps along the gender axis, which ranged from -3 SD (female) to +1 SD (male). Thus, the stimuli used in the adaptation experiments were centered on the walker that appeared to be perceptually neutral in the baseline experiment.

Point-light displays were presented in frontal orthographic projection as white dots on a black background using a 17-in. CRT monitor. Image generation was synchronized to the monitor's 75-Hz refresh rate. Walkers subtended 5×9 deg of visual angle at a viewing distance of 75 cm.

Procedure

In the first part of the experiment, we recorded participants' responses to the different walkers without adaptation. In each of these baseline (nonadaptation) trials, participants viewed a single point-light walker for a variable exposure duration of 350 ms, 700 ms, 1.4 s, 3.5 s, or 7 s. One motivation for this experiment was to make sure that perceived gender did not depend on presentation time per se. The chosen exposure durations therefore covered a large part of the range used later for testing and for adaptation. Here, as well in the subsequent adaptation trials (see below), the participants' task was to report whether the walker appeared male or female (2AFC design). Responses were given by pressing one of two keys on a computer's keyboard. Participants conducted six sessions with 325 trials each (13 levels along the gender axis \times 5 levels of exposure duration \times 5 repetitions), resulting in a total of 1,950 trials per participant. The order of the trials within a session was randomized. Individual trials were separated by a 4-s intertrial interval during which the screen remained blank. The six sessions were spread over at least 2 days. Breaks between sessions lasted at least 10 min.

In the subsequent adaptation trials, the above design was augmented by having the participant first view an adapting stimulus—the exaggerated female, male, or neutral walkers (see Stimuli section)—for a set adaptation duration, followed by a storage duration during which the screen remained blank, and finally by the presentation of the test stimulus (a walker generated at one of seven equidistant steps along the gender axis), presented for a set test duration. The 4-s intertrial intervals between all adaptation trials were filled with a mask of 1,000 randomly moving dots.

This simple adaptation paradigm allowed for independent manipulation of three different temporal parameters: the adaptation duration (3.5, 7, and 14 s), the storage duration (0 ms, 200 ms, 600 ms, 1.2 s, and 2.4 s), and the test duration (350 ms, 700 ms, and 1.4 s). In all trials in which adaptation duration was manipulated, the storage duration was held constant at 200 ms and the test duration at 700 ms; when storage duration was varied, the adaptation duration was held at 7 s and the test duration at 700 ms; and when test duration was varied, the adaptation duration for adaptation, storage, and test were chosen to cover a range within which we hoped to capture most of the dynamics of the buildup and decay of the adaptive state and were based on preceding pilot studies.

Trials were blocked into sessions in which only one of the three variables of interest varied. Each participant conducted 18 sessions altogether, held in approximately 8 to 10 days over a period of 4 weeks. During the first 6 sessions, adaptation time was varied. Each session contained 126 trials (three types of adapting stimuli, seven probes along the gender axis, three types of adaptation durations, two repetitions of each combination). In the next 6 sessions, storage time was varied (210 trials: $3 \times 7 \times$ 5×2), and in the last 6 sessions, test duration was varied ($3 \times 7 \times 3 \times 2 = 126$ trials).

Data processing

The raw psychophysical data from each participant was fit with a sigmoid Boltzmann function. Modeling the proportion of "female" responses y, this function has the form $y = 1/(1 + \exp((x - x_0)/w))$, where x_0 is the midpoint of the function and w parameterizes its width. The midpoint of the Boltzmann function was used as a measure for the point of subjective equality (PSE) at which participants rated a walker to be female in 50% of the cases. The negative slope of the function at the midpoint (d = 1/4w) was taken as a measure for the discriminability of male and female walkers. PSEs and discriminabilities were subject to further group averaging and ANOVA.

Results

Figures 1a and 1b show the average PSE and discriminability values, as well as their standard errors, for the baseline (nonadaptation) trials, plotted as a function of exposure duration. For these baseline trials, a one-way ANOVA confirmed that there was a significant effect of exposure duration on discriminability, F(4,68) = 10.95, p < .001, with longer exposure duration leading to a greater discriminability. The measures of PSE, however, showed no effect of exposure duration, F(4,68) = 0.93. Notably, this avoids concern that such an effect could contaminate the results of the adaptation trials. The observation that the perceptually gender-neutral walker was more female (i.e., a nonzero, negative PSE) than the mathematically average walker guided the selection of the adapting walkers and testing range for the adaptation trials (see Stimuli section).

Figure 2 shows one participant's raw data (mean and standard error) and fit Boltzmann function to demonstrate



Figure 1. Results of baseline (no adaptation) measurements. Means and standard errors (n = 18) of (a) PSE and (b) discriminability for different presentation durations.



Figure 2. Means and standard errors (n = 36) of the ratings of one individual participant for the trials in which adaptation duration was manipulated. Black, blue, and red curves correspond to responses after neutral, male, and female adaptation, respectively.

data processing and to illustrate the general adaptation effect found in all the adaptation tests (i.e., regardless of whether adaptation, storage, or test duration was manipulated), in this case for trials where adaptation duration was manipulated. The vertical axis indicates the proportion of "female" responses (1 = all "female" responses, 0 = all"male" responses), and the horizontal axis corresponds to the gender axis. The black curve (and raw data) indicates the participant's responses to the test stimuli when the adapting stimulus was the neutral walker. The blue curve reveals the shift in these responses, toward more "female" reports, that occurred for test stimuli following the male adapting stimulus. Conversely, the red curve demonstrates the reverse effect: The participant was more likely to perceive the test stimuli as "male" following adaptation to the female adapting stimulus.

A different illustration of this adaptation effect is shown in Figure 3, where the data from all participants is compiled for all trials where storage duration was manipulated. To highlight the PSE shifts following male or female adaptation, we subtracted PSE values for neutral adaptation from the corresponding PSEs for the male and female adapting stimulus; as such, this histogram explicitly depicts the PSE shifts (i.e., differences), relative to the neutral adaptation case, following male (blue) or female (red) adaptation.

For all adaptation trials, two-way repeated measures ANOVAs (testing the effect of the adapting stimulus and of the manipulated temporal variable) confirmed a significant main effect of the adapting stimulus on the PSE, irrespective of whether the data were from trials where the manipulated temporal variable was adaptation duration, F(2,22) = 12.75, p < .001, storage duration,

F(2,22) = 27.35, p < .001, or test duration, F(2,22) = 23.81, p < .001.

On average, over all trials, the absolute difference between the PSEs obtained after neutral and after female adaptation amounted to 0.36 SD, one sample t test: t(11) = 3.48, p < .01, whereas the difference after male adaptation was 0.69 SD, t(11) = 5.89, p < .001. A paired-samples t test confirms that the induced PSE shift after male adaptation is in fact significantly higher than that after female adaptation, t(11) = 3.58, p < .005.

The two-way ANOVAs mentioned above also tested whether the manipulations of the temporal variables (adaptation, storage, and test durations) had any effects on PSEs and whether there were any interactions between these factors and the adaptation stimulus. Figure 4 shows the PSEs following male, neutral, and female adaptation plotted as functions of adaptation, storage, and test durations. A main effect was only found for storage duration, F(4,44) = 7.30, p < .001. PSEs were more negative for shorter storage durations; that is, at very short (and particularly at zero) storage duration, there was an overall bias for participants to be more likely to provide "male" responses in all adaptation conditions.

Interactions with the type of adaptation stimulus were found for adaptation duration, F(4,44) = 5.17, p < .005, and test duration, F(4,44) = 3.13, p < .05. The effect of the adaptation stimulus increased with longer adaptation durations and decreased with longer test durations.

Similarly designed two-way repeated measures ANOVAs were also run to investigate effects on discriminability. As in the first experiment, discriminability increased with increasing test duration, F(2,22) = 4.98,



Figure 3. Histogram of PSE shifts following male (blue) and female (red) adapting stimuli, shown relative to neutral adapting stimulus (black dotted line at 0). Data collapsed across all trials manipulating storage duration.



Figure 4. Means and standard errors of PSEs following adaptation to male (blue), neutral (black), or female (red) walkers, shown as functions of manipulated adaptation, storage, and test duration. Recall that based on the results of the first experiment, the perceptually neutral walker was defined to be a walker with a *z* score of -1, the adapting male walker corresponded to 5 *SD*, and the adapting female walker to -7 *SD*.

p < .05. All other main effects and all interactions were not significant.

Discussion

The above results show a clear influence of the adapting stimulus on the perceived gender of the test stimulus: A significant main effect of the adapting stimulus was seen on the PSE regardless of whether the analysis incorporated data from trials where adaptation, storage, or test duration was varied. In line with our original expectations, the observed modifications in perceived gender were of an opponent nature: Adaptation to female biological motion caused the following point-light walker to appear more male than it would have otherwise and vice versa. This observation adds another high-level visual domain to the list of perceptual phenomena influenced by adaptation aftereffects. However, although gender recognition from biological motion seems to be a relatively sophisticated, high-level visual ability, adaptation and the corresponding aftereffect might still operate on a much lower level. The dots constituting the point-light displays are characterized by properties such as an average location, the frequency of the oscillatory movement about that location, amplitude and direction forming the shape of the trajectory, and so forth. All these attributes are intrinsically low level and potentially subject to adaptation effects, the sum of which could well result in modifications of "high-level" classification like the ones we observed here for perceived gender.

However, adaptation could as well operate on a representational level at which the low-level cues are already integrated into more complex features that represent the shape, the kinematics, and the dynamics of a moving human body. On this level, the visual system might encode features such as body sway, shoulder–hip ratio, overall vertical body movement, and so forth, many of which are indicative of a walker's gender. Adaptation on this level could also result in aftereffects like the ones observed in our experiments. The information from such midlevel features could be integrated in terms of distributed neural population codes or converge on some kind of "gender-opponent" representation. Either representation could be subject to adaptation and result in aftereffects.

While these stages are perceptual, modifications of an observers response behavior could also be due to response strategies that are not directly related to the particular stimulus but rather to its contents and significance. If an observer would expect—for whatever reason—that the presentation of a man is followed by a woman and vice versa, we would also expect to observe "aftereffects." In this case, they would not be due to perceptual adaptation but rather to expectations on a cognitive level.

Our data are important in demonstrating that there are strong aftereffects in the context of gender classification from biological motion, but they are not yet able to distinguish on which representational level they occur. This question could potentially be answered by employing generalization experiments to investigate how robust the observed aftereffects are with respect to changes in position, size, and three-dimensional orientation of the point-light displays and whether adaptation with point-light displays creates aftereffects with stick figures, realistic renderings of walkers, or even completely different classes of stimuli such as male and female faces.

The dependencies on the durations of adaptation, storage, and testing are not as pronounced as in studies on other adaptation aftereffects, but they show the same general tendency. The aftereffect increases with longer adaptation time, and it decreases with longer test times. For the storage time, our data did not reveal a statistically significant effect. However, the trend observed in Figure 4 implies that there might be a decrease in the aftereffect with increasing storage time that we missed to document because the maximum storage time was not large enough.

In addition to the pronounced effect of adaptation on a trial-by-trial basis, we observed adaptation to the range of stimuli used in the experiment. In the first sessions in which we had measured baseline perception without adaptation, psychometric functions were shifted, showing a bias to respond "male." On the basis of this finding, we chose the adaptation stimuli and the range of test stimuli for the subsequent adaptation sessions to be roughly centered on the perceptually neutral walker that deviated from the mathematically neutral walker by almost 1 *SD*. However, as can be seen from Figure 4, this did not produce the expected result. In the conditions with (perceptually) neutral adaptation, the PSE has now shifted even further into the female part of the spectrum. Although a stimulus located 1 *SD*

away from the average walker in the female part of the spectrum was enough to produce a perceptually neutral walker in the baseline sessions, about 1.7 *SD* was required in the "neutral" condition of the adaptation sessions. It seems that there is a general bias toward seeing more male than female walkers in a set of stimuli and that adaptation to the range of stimuli used keeps this bias almost constant. Further research has to verify if this assumption is true and what the causes of the observed "male bias" are.

The very robust adaptation effects observed on a trial-bytrial basis and in terms of a range effect present a number of interesting questions for future study.

First, the relative contributions of structural versus kinematic cues to this adaptation effect remain to be investigated. With the framework described by Troje (2002a), one could test this question by explicitly dissociating the structural and kinematic parameters defining the point-light walkers, for example, creating walkers that move identically but have sexually dimorphic body frames and vice versa. As discussed above, another question concerns the extent to which this adaptation effect can be considered a low- or high-level phenomenon (or, perhaps both, as suggested by Thornton, Pinot, & Shiffrar, 1998, for other aspects of biological motion perception). This question is closely related to the issue of generalization, that is, the extent to which one would expect the aftereffect to be observed in a test stimulus that differs from the adapting stimulus along various dimensions. To make these assessments, simple variations on our current experiments could be conducted where the adapting and test stimuli differ in their location, size, orientation, viewpoint (i.e., three-dimensional rotation), speed, the eye with which they are viewed, and so on.

Aftereffects provide a very powerful tool to decouple the stimulus itself from its perception. In particular, because a participant's perceptual response to a given stimulus, for instance, the gender-neutral averaged walker, can show striking and reliable variation based on perceptual history alone, we can see that the participant's percept may be partly decoupled from the properties of the proximal stimulus. As such, various other measures of response, including neural activity, could be linked more clearly to the higher level percept and not the particulars of the stimulus. A similar idea lay behind a recent proposal by Sadr and Sinha (2004) for exploiting a marked hysteresis effect observed in object and face perception. For example, using a neuroimaging technique, a comparison between "male" and "female" perceptual responses, in which the test stimulus had always been the neutral walker, would be expected to reveal only the activity associated with the higher level gender percept, whereas other activities, linked only to low-level stimulus properties, would be removed from the analysis.

Conversely, one could imagine a markedly different situation if the perceptual adaptation coincided with significant neural adaptation observed at various areas/levels in the visual system—a likely possibility given the neuroimaging work by Culham et al. (1999), Kohn and Movshon (2003),

and Tootell et al. (1995) in studies of other, simpler cases of motion adaptation. One could ask at the outset, then, whether the adaptation effects observed in the current study might have neural correlates in relatively "lower" visual motion areas and/or if this sort of differential neural activity might be observed in "higher" areas specifically associated with the perception of biological motion (e.g., Grossman et al., 2000). As a matter of fact, the phenomena of neural adaptation and recovery could, by themselves, facilitate such research. Recent studies, beginning with Kourtzi and Kanwisher's (2000, 2001) on shape perception and the lateral occipital complex, have utilized a technique whereby repeated, habituating presentations of a given stimulus are followed by a new stimulus. Neural responses decline with each presentation of the first stimulus, and a specific locus of activity corresponding to the elevated neural activity elicited by the new stimulus can be isolated. This view of very specific neural populations is supported by Rhodes et al. (2004) who reported opposite direction face aftereffects for upright and inverted faces. This approach can specifically examine the extent to which the visual machinery in question is sensitive to different variations between stimuli. For the example of biological motion, one could imagine testing the extent to which differences in a point-light walker's gender, static and dynamic features, size, orientation, and so forth, are "detected" by different neural populations of interest and so stimulate recovery from neural adaptation. In some ways, one could think of this as a neural counterpart of the behavioral generalization studies discussed above.

Conclusions

In this work, we report on a robust adaptation aftereffect in the perception of gender in biological motion. Adaptation to a male stimulus biases the viewer toward a subsequent female percept (and vice versa). The observed aftereffects increase with adaptation time and decrease with the duration of the test stimulus—a feature that distinguishes true adaptation effects from simple priming effects. We believe that this finding, and continuing work using variations on this approach, may shed light on important properties of the representations and mechanisms underlying biological motion perception. The results also lend further support to the perceptual and psychological merits and validity of the mathematical approach used to extract and represent the "gender axis" investigated in this study and in Troje (2002a, 2002b).

Acknowledgments

The authors would like to thank Patrick Cavanagh and Martin Giese for helpful comments on this work and Tobias by the Volkswagen Foundation and the Canada Foundation for Innovation. J. Sadr and K. Nakayama were funded in part by an NSF grant in Human and Social Dynamics (HSD-DHB-MOD Grant #135925-346629-0001-51681).

Commercial relationships: none. Corresponding author: Nikolaus Troje. Email: troje@post.queensu.ca. Address: 62 Arch St., Kingston, Ontario, Canada K7L3N6.

References

Troie et al.

- Barclay, C. D., Cutting, J. E., & Kozlowski, L. T. (1978). Temporal and spatial factors in gait perception that influence gender recognition. *Perception & Psychophysics*, 23, 145–152. [PubMed]
- Blanz, V., & Vetter, T. (1999) A morphable model for the synthesis of 3D Faces. In Symposium on Interactive 3D Graphics—Proceedings of SIGGRAPH '99 (pp. 187–194). New York: ACM Press.
- Clifford, C. W., Wenderoth, P., & Spehar, B. (2000). A functional angle on some after-effects in cortical vision. *Proceedings: Biological Sciences/The Royal Society*, 267, 1705–1710. [PubMed] [Article]
- Culham, J. C., Dukelow, S. P., Vilis, T., Hassard, F. A., Gati, J. S., Menon, R. S., et al. (1999). Recovery of fMRI activation in motion area MT following storage of the motion aftereffect. *Journal of Neurophysiology*, *81*, 388–393. [PubMed] [Article]
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal* of Cognitive Neuroscience, 12, 711–720. [PubMed]
- Hershenson, M. (1989) Duration, time constant, and decay of the linear motion aftereffect as a function of inspection duration. *Perception & Psychophysics*, 45, 251–257. [PubMed]
- Hsu, S. M., & Young, A. W. (2004). Adaptation effects in facial expression recognition. *Visual Cognition*, *11*, 871–899.
- Jacobs, A., & Shiffrar, M. (2005). Walking perception by walking observers. *Journal of Experimental Psychology: Human Perception and Performance*, 31, 157–169. [PubMed]
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, 14, 201–211.
- Johansson, G. (1975). Visual motion perception. *Scientific American*, 232, 76–88. [PubMed]
- Kohn, A., & Movshon, J. A. (2003). Neuronal adaptation to visual motion in area MT of the macaque. *Neuron*, 39, 681–691. [PubMed] [Article]

- Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *The Journal* of *Neuroscience*, 20, 3310–3318. [PubMed] [Article]
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, 293, 1506–1509. [PubMed]
- Kozlowski, L. T., & Cutting, J. E. (1977). Recognizing the sex of a walker from a dynamic point-light display. *Perception & Psychophysics*, 21, 575–580.
- Kozlowski, L. T., & Cutting, J. E. (1978). Recognizing the gender of walkers from point-lights mounted on ankles: Some second thoughts. *Perception & Psychophysics*, 23, 459.
- 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. [PubMed] [Article]
- Leopold, D. A., Rhodes, G., Müller, K. M, & Jeffrey, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 272, 897–904. [PubMed] [Article]
- Mather, G., & Murdoch, L. (1994). Gender discrimination in biological motion displays based on dynamic cues. *Proceedings of the Royal Society of London. Series B*, *Biological Sciences*, 258, 273–279.
- Nilsson, L. G., Olofsson, U., & Nyberg, L. (1992). Implicit memory of dynamic information. *Bulletin of the Psychonomic Society*, 30, 265–267.
- Olofsson, U., Nyberg, L., & Nilsson, L. G. (1997). Priming and recognition of human motion patterns. *Visual Cognition*, *4*, 373–382.
- Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W., & Nakayama, K. (2003). Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychological Science*, 14, 558–566. [PubMed]
- Rhodes, G., Jeffrey, L., Watson, T. L., Jaquet, E., Winkler, C., & Clifford, C. W. (2004). Orientation-contingent face aftereffects and implications for face-coding mechanisms. *Current Biology*, 14, 2119–2123. [PubMed] [Article]
- Runeson, S., & Frykholm, G. (1983). Kinematic specification of dynamics as an informational basis for person-and-action perception: Expectation, gender recognition, and deceptive intention. *Journal of Experimental Psychology: General*, 112, 585–615.
- Sadr, J., & Sinha, P. (2004). Object recognition and random image structure evolution. *Cognitive Science*, 28, 259–287.

- Thornton, I. M., Pinot, J., & Shiffrar, M. (1998). The visual perception of human locomotion. *Cognitive Neuropsychology*, 15, 535–552.
- Thornton, I. M., & Vuong, Q. C. (2004). Incidental processing of biological motion. *Current Biology*, 14, 1084–1089. [PubMed] [Article]
- Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., et al. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature*, 375, 139–141. [PubMed]
- Troje, N. F. (2002a). Decomposing biological motion: A framework for analysis and synthesis of human gait patterns. *Journal of Vision*, 2(5), 371–387, http://journalofvision.org/2/5/2/, doi:10.1167/2.5.2. [PubMed] [Article]
- Troje, N. F. (2002b). The little difference: Fourier based gender classification from biological motion. In R. P. Würtz & M. Lappe (Eds.), *Dynamic perception* (pp. 115–120). Berlin: Aka Verlag.
- Troje, N. F., & Geyer, H. (2002). After-effects in biological motion perception [Abstract]. *European Conference of Visual Perception (ECVP)*, Glasgow.
- Verfaillie, K. (2000). Perceiving human locomotion: Priming effects in direction discrimination. Brain and Cognition, 44, 192–213. [PubMed]
- Vetter, T., & Troje, N. F. (1997). Separation of texture and shape in images of faces for image coding and synthesis. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 14*, 2152–2161.
- Wade, N. J., & Verstraten, F. A. J. (1998). Introduction and historical overview. In G. Mather, F. A. J. Verstraten, & S. Anstis (Eds.), *The motion aftereffect: A modern perspective* (pp. 1–23). Cambridge, MA: MIT Press.
- Watson, T. L., & Clifford, C. W. (2003). Pulling faces: An investigation of the face-distortion aftereffect. *Perception*, 32, 1109–1116. [PubMed]
- Webster, M. A. (1996). Human colour perception and its adaptation. *Network: Computation in Neural Systems*, 7, 587–634.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural face categories. *Nature*, 428, 557–561. [PubMed]
- Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, 6, 647–653. [PubMed]
- Zhao, L., & Chubb, C. (2001). The size-tuning of the face-distortion after-effect. *Vision Research*, *41*, 2979–2994. [PubMed]