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# Spontaneous recovery and time course of biological motion adaptation

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#### ABSTRACT

Adaptation to changes of the environment is an essential function of the visual system. Recent studies have revealed that prolonged viewing of a point-light display of a human walker can produce the perception of a point-light walker facing in the opposite direction in a subsequent ambiguous test. Similar effects of biological motion adaptation have been documented for various properties of the point-light walkers. However, the time course and controlling mechanisms for biological motion adaptation have not yet been examined. The present study investigated whether a single mechanism or multiple mechanisms controlled biological motion adaptation. In Experiment 1, a relatively long duration of initial adaptation to one facing direction of a point-light walker of the opposite facing direction. Chimeric ambiguous walkers were used to test the aftereffect in a top-up manner. We observed spontaneous recovery of the adaptation adaptation that accorded well with the duration scaling law (i.e., effects of adaptation become stronger and longer-lasting as adaptation duration increases). Further analysis indicated that the slower but not the faster component of the adaptation effects complied with the law. These findings suggest that biological motion adaptation is controlled by the multiple mechanisms tuned to differing timescales.

#### 1. Introduction

Visual adaptation is a well-known process describing prolonged viewing of visual stimuli producing pronounced negative aftereffects. It allows the visual system to maintain high sensitivity to the ever-changing environment (for reviews, see Kohn, 2007; Webster, 2011, 2015), and has been found at both the lower and higher levels of visual processing. For example, an ambiguous point-light walker in gender is readily perceived to be male after prolonged viewing of an exaggerated female point-light walker, a phenomenon referred to as biological motion adaptation (Jordan, Fallah, & Stoner, 2006; Troje, Sadr, Geyer, & Nakayama, 2006).

Biological motion aftereffects have been frequently reported from various aspects of point-light displays of human actors, such as gender (Hiris, Mirenzi, & Janis, 2016; Jordan et al., 2006; Troje et al., 2006), emotion (Mazzoni, Jacobs, Venuti, Silvanto, & Cattaneo, 2017; Roether, Omlor, Christensen, & Giese, 2009), viewpoint (Benton, Thirkettle, & Scott-Samuel, 2016), walking direction (e.g., forward- or backwardwalking movement) (Barraclough & Jellema, 2011; Stephan, Mina, & Bülthoff, 2016; Theusner, de Lussanet, & Lappe, 2011), facing direction (e.g., leftward- or rightward-facing movement) (Jackson & Blake, 2010; Theusner et al., 2011), and running versus walking (Van Boxtel, Dapretto, & Lu, 2016; Van Boxtel & Lu, 2013). However, the temporal dynamics and controlling mechanisms of biological motion adaptation, to our knowledge, have not yet been investigated.

Previous studies have shown that effects of adaptation become stronger and longer-lasting as adaptation durations increase. This duration scaling law has been documented for McCollough effect (Vul, Krizay, & Macleod, 2008) and contrast adaptation (Bao & Engel, 2012; Greenlee, Georgeson, Magnussen, & Harris, 1991). One theory assumes that a single neural mechanism operating at different timescales controls the temporal dynamics of visual adaptation (Grzywacz & Juan, 2003; Wark, Fairhall, & Rieke, 2009). However, recent work has disclosed that visual adaptation could be controlled by multiple distinct mechanisms operating over differing timescales (e.g., slow and fast timescales) (Bao & Engel, 2012; Bao, Fast, Mesik, & Engel, 2013; Mei, Dong, Dong, & Bao, 2015; Mesik, Bao, & Engel, 2013; Tregillus, Werner, & Webster, 2016; Vul et al., 2008). By means of a "deadaptation" paradigm, these studies disclose the "spontaneous recovery" of adaptation effects which supports the multiple mechanisms theory.

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In the deadaptation paradigm, effects of initial adaptation for a relatively long duration are extinguished by subsequent adaptation for a relatively short duration that produces the opposite aftereffects. For example, in a study on motion aftereffect (Mesik et al., 2013), subjects adapted to the leftward drifting gratings for 10 min in the initial adaptation period, and then deadapted to the rightward drifting gratings for a relatively short period. In the subsequent post-test, the subjects viewed a physically static display. They reported first seeing a static display and later perceiving gradually conspicuous rightward motion induced by the initial adaptation. This spontaneous recovery phenomenon attests the existence of multiple temporally-tuned me chanisms controlling visual adaptation.

In the present study, we aim to examine whether the spontaneous recovery phenomenon also exists in biological motion adaptation. Therefore, a deadaptation paradigm was adopted in Experiment 1. Experiment 2 further examined whether biological motion adaptation complied with the duration scaling law (i.e., adaptation effects become stronger and longer-lasting as adaptation duration increases). Our results in both experiments support the multiple mechanisms theory of visual adaptation, indicating that the theory may generally account for the temporal dynamics of visual adaptation.

#### 2. Experiment 1

#### 2.1. Methods

#### 2.1.1. Participants

Twelve subjects (seven females, 19-35 years old, mean age = 22.8 years, SD = 4.2) participated in Experiment 1. For Experiment 1 and 2, all subjects had normal or corrected-normal vision, and were naïve to the purpose of the experiments, except one of the authors (G.M.) who only participated in Experiment 1. The subjects gave written informed consent and were paid for participating. Experimental procedures were approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences, and conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki).

#### 2.1.2. Apparatus

Stimuli were presented on a gamma-corrected 21-in. Philips 201P10 CRT monitor, with a resolution of  $1024 \times 768$  pixels, a refresh rate of 60 Hz, and a mean luminance of approximately  $38 \text{ cd/m}^2$ . Subjects viewed the screen from a distance of 100 cm in a dark room. A head and chin rest were used to maintain the constant viewing distance and help minimize head movement. The stimuli were displayed using the PsychToolbox-3 (Brainard, 1997; Pelli, 1997) in MATLAB (MathWorks, Natick, MA).

#### 2.1.3. Stimuli

A point-light walker (PLW) stimulus was generated from motion capture data of a male human walker, which was acquired from the Carnegie Mellon Graphics Lab Motion Capture Database (freely available: http://mocap.cs.cmu.edu). We used the BioMotion Toolbox (van Boxtel & Lu, 2013), based upon the MATLAB environment, to manipulate the motion capture data and specify the action displays (Su & Lu, 2017; Van Boxtel, Peng, Su, & Lu, 2016). The toolbox was firstly used to convert raw c3d motion capture files (document number: 132\_18.c3d) to the point-light format, and consequently the created PLW appeared to walk forward on a treadmill. There are a total of 41 light points in the original Databases' PLW, and in the present study the stimuli consisted of a selected 20 out of those 41 light points, representing the main joints such as the shoulders and feet. In order to obtain a continuous walking action, 95 animation frames from the 235th to the 329th frame (i.e., a walking cycle took approximately 1.6 s) were extracted from 425 animation frames of the raw PLW stimulus. Further, the Smoothloop function of the BioMotion Toolbox was used to help smooth transition



**Fig. 1.** The schematic description of the trial procedure for Experiment 1. In each trial, the PLW or scrambled adapter was presented for 4.8 s, followed by a 1-s blank ISI, and then the test stimulus (blue chimeric ambiguous walkers) was presented for 1 s. During the top-up adaptation, at the moment when the green adapter briefly became red, the subjects were asked to press the space button with their left hand. When the blue test stimulus cued by a brief beep appeared, the subjects reported their first impression of facing direction of the test stimulus by pressing one of two buttons with their right hand (a two-alternative-forced-choice task, 2AFC). The lines composing a human form were not actually displayed in the experiments, and were here plotted for demonstration purposes only. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

from the last frame back to the first frame, so that the looping of the PLW stimulus was nearly imperceptible.

To avoid potential effects of local motion signals to adaptation aftereffects specific to biological motion processing, we used the Limitedlife function of the BioMotion Toolbox to produce limited-life PLW stimuli (Beintema, Georg, & Lappe, 2006; Beintema & Lappe, 2002), instead of the classic PLW stimuli (Johansson, 1973; Troje, 2002; Wang, Zhang, He, & Jiang, 2010; Wang et al., 2018). For each animation frame, the dots of limited-life PLW were randomly distributed on the limb along the skeleton, and their spatial locations were reallocated for the next animation frame. An animation frame included 20 light-points, and lasted for approximately 16.7 ms.

Experiment 1 included the PLW and the position-scrambled PLW adaptation condition. The latter was designed to test whether in the current paradigm position-scrambled adapters would induce a significant biological motion aftereffect on account of other factors such as fatigue (Mei et al., 2015). The adapter stimulus in the PLW adaptation condition was a leftward- or rightward PLW (see Fig. 1); the position-scrambled adapter in the scrambling condition was generated by means of the Scramble function of the BioMotion Toolbox. The limited-life PLW adapters were easily recognized as a walker by the subjects. The scrambled adapter had the same point-light motions as the PLW in the adaptation condition, but did not have human form. All adapters included 20 light-points.

Following the previous studies (Theusner et al., 2011; Thornton, 2003), we used chimeric ambiguous walkers as the test stimuli consisting of two superimposed walkers with opposite facing directions

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