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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 was followed by a relatively short duration of deadaptation in which the adapter was 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 effects in the post-test period. The Experiment 2 further delineated the build-up and decay of biological motion 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 backward-walking 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 mechanisms 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 × 768 pixels, a refresh rate of 60 Hz, and a mean luminance of approximately 38 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 from the last frame back to the first frame, so that the looping of the PLW stimulus was nearly imperceptible.

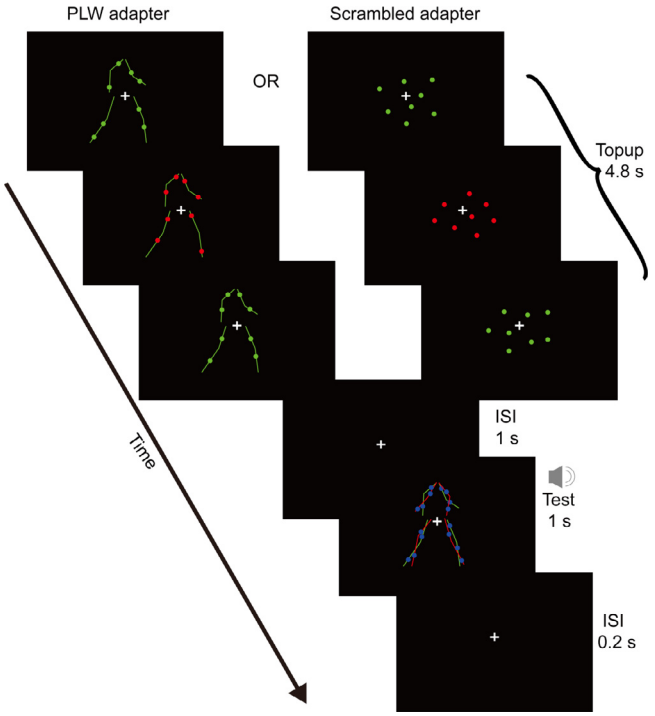

Fig. 1. The schematic description of the trial procedure for Experiment 1. In each trial, the PLW or scrambled adapter was presented for 4.8 s, followed by a 1-s blank ISI, and then the test stimulus (blue chimeric ambiguous walkers) was presented for 1 s. During the top-up adaptation, at the moment 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.)

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

(see Fig. 1). The whole test stimuli (two walkers) included 20 light-points in total, and the numbers of light-points of each walker were redistributed for each trial, according to a one-down-one up staircase procedure (see the Procedure section for details). Thus, in each trial, the degree of ambiguity of the test stimuli (i.e., leftward- or rightward-facing) was changed. For example, the subjects would perceive the chimeric walkers facing to the left side when more light-points (e.g., 14 points) were assigned to the body of the leftward-facing walkers than to the body of the rightward-facing walkers (e.g., 6 points). The adaptation effects can be described by the percentage of points assigned to the body of the two walkers (e.g., 14/20). The same test stimuli were used for both the PLW adaptation condition and the scrambled control condition (see Fig. 1).

The adapters and test stimuli consisted of green and blue points on a black background, respectively. To make the subjects pay attention to the adapter during the top-up adaptation in each trial, we asked them to press the space button with the left hand when the color of the adapter changed from green to red (see Fig. 1). This red adapter only lasted for 200 ms, and randomly appeared between 1.5 s and 3.3 s in a 4.8-s top-up adaptation duration. The height of the PLW stimulus was about 6.5°, and dot size was 6 pixels in diameter. Both adapters and test stimuli were presented at the center of the monitor.

2.1.4. Procedure

Following the previous work (Bao et al., 2013; Mei et al., 2015; Mesik et al., 2013; Vul et al., 2008), we used a top-up paradigm to track the time course of biological motion adaptation and a "deadaptation" method to observe the spontaneous recovery of adaptation effects.

There were four stages for each session in Experiment 1 (see Fig. 2A): (i) a 150-s "baseline" period without adapters (75 trials with 2 s for each trial), (ii) a 301-s "adaptation" period with a leftward/rightward PLW or a scrambled adapter (43 trials with 7 s for each trial), (iii) a "deadaptation" period with a rightward/leftward PLW or a scrambled adapter (7 s for each trial), and (iv) a 240-s "post-test" period without adapters (120 trials with 2 s for each trial). For each session, the "deadaptation" period was terminated whenever the percentage of points that belong to the component walker of the adaptation direction was lower than the baseline (see the Analysis section for baseline estimation) or the duration of deadaptation exceeded 126 s (ie., 18 trials). Note that, for the PLW adaptation condition, the facing direction of the adapters in the adaptation stage was opposite to that of the adapters in the deadaptation stage. For the scrambled PLW adaptation condition, the deadaptation stimuli were scrambled PLWs derived from PLWs facing in the opposite direction (e.g., the light points of a rightward-facing walker were scrambled to produce a rightward scrambled PLW adapter, and the deadaptation stimulus was a leftward scrambled PLW).

In each trial of the adaptation and deadaptation periods (see Fig. 1), a top-up adapter was presented for 4.8 s. After a 1-s blank interval, the test stimulus, which was cued by a brief beep, was presented for 1 s. The next trial started after a 0.2-s blank interval. And, in each trial of the baseline and post-test periods, the test stimulus was presented for 1 s, followed by a 1-s blank interval. The same ambiguous chimeric walkers and staircase procedure were used in the baseline and post-test periods of a session. The central fixation point was presented throughout the session.

Subjects performed a two-alternative-forced-choice (2AFC) task. For each trial, they were asked to report the facing direction of the test stimulus (i.e., leftward or rightward) based on their first impression by pressing one of two buttons with their right hand. Subjects were encouraged to guess the facing direction when they could not discern the direction. The percentage of points for each component walker of the test stimulus began with 50% (i.e., two superimposed walkers consisting of 10 points respectively), and was adjusted through a one-down-one-up staircase procedure. Because the light points composing one walker of the chimeric test stimulus were allowed to vary from 0 to 20 points, available testing stimuli totally had 21 levels. The initial step size of the staircase was three levels. After three reversals, the step size reduced to two levels, and to one level after another three reversals. Throughout the experiments, subjects were required to stare at the central fixation point.

All subjects completed eight sessions for each facing direction (leftward or rightward) of the adapters, and an additional sixteen sessions for the position-scrambled condition. These thirty-two sessions in total were tested in a randomized order. Subjects were required to take a break for at least one hour between two successive sessions.

2.2. Analysis

The baseline of each session was estimated by averaging the percentage of points of the last 10 reversals of the test stimuli in the "baseline" period. To normalize the data and combine the adaptation effects of the leftward and rightward adaptation directions, we then subtracted the baseline from the raw timeseries. To evaluate the adaptation effect, the percentage of points of the last 5 reversals of the test stimuli in the adaptation period was averaged. We then compared the adaptation effect with zero using one-sample *t*-test. The time series of percentage of points of test stimuli were interpolated by the nearest-neighbor method at a 2 s sample interval for the baseline and post-test periods and a 7 s sample interval for the adaptation and deadaptation periods, and were then averaged across sessions. To examine whether the spontaneous recovery would emerge, we performed a linear trend analysis with respect to the normalized time course from the starting time to the peak time of the post-test period. This analysis method has previously been used in the deadaptation paradigm (Bao & Engel, 2012;

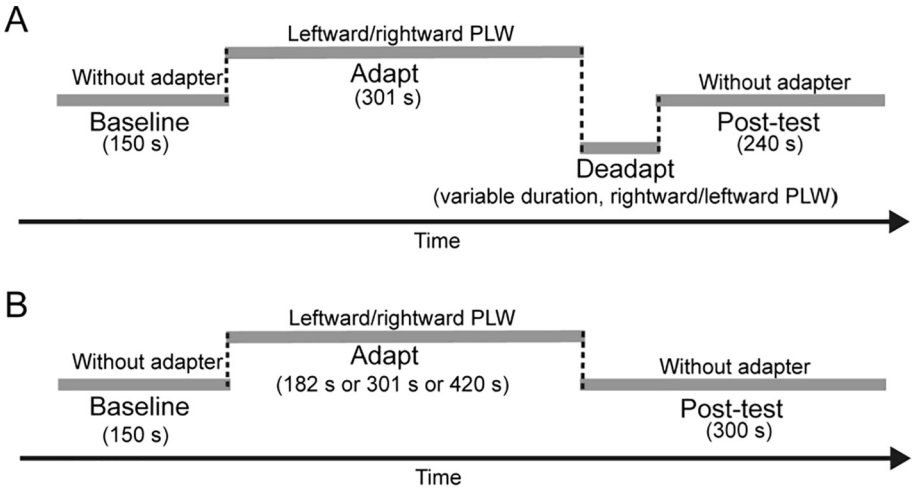

Fig. 2. The procedure of each session for the Experiment 1 (A) and the Experiment 2 (B). Each session of Experiment 1 included four stages: a "baseline" stage without adapters, an "adaptation" stage with leftward or rightward point-light walkers (adapters), a "deadaptation" stage with rightward or leftward point-light walkers (deadapters), and a "post-test" stage without adapters. Notably, the adapters and deadapters moved in the opposite directions, and thus created the opposing adaptation aftereffects. The procedure of Experiment 2 was similar to that of Experiment 1 except that a "deadaptation" stage was removed, duration in the "post-test" stage was extended to 300 s, and adaptation durations of 182 s, 301 s and 420 s were used across conditions. For both experiments, the deadaptation duration was varied in each session (see Procedure for details).

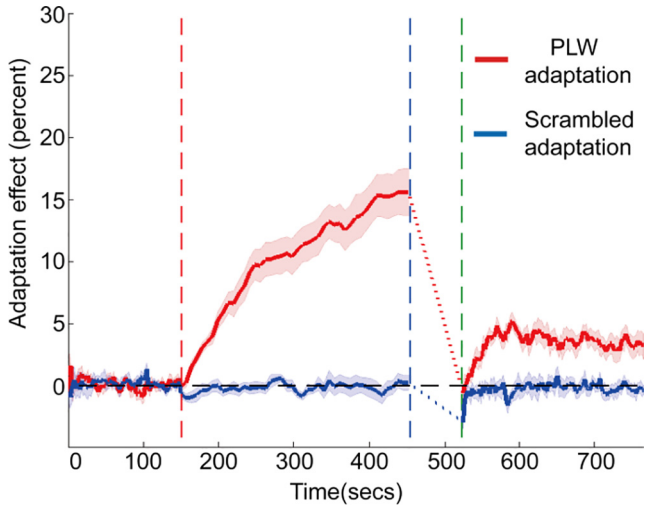

Fig. 3. Grand average time courses for the point-light walkers (PLWs) and position-scrambled adaptation conditions in Experiment 1. Adaptation effects were normalized by subtracting average corresponding percentage of points of the last 10 reversals of the test stimuli in the baseline period. Red and blue curves correspond to the grand average time courses of adaptation effects for the PLW and position-scrambled adapter stimuli, respectively. Shaded regions show ± one standard error of the mean across subjects. The three vertical dashed lines represent the start times of the adaptation, deadaptation and post-test periods, respectively. Because the deadaptation duration were various across sessions, deadaptation curves are replaced with dashed lines. To inspect the time course of deadaptation, we presented several example sessions showing raw data of the deadaptation periods in the Supplementary Materials (Figs. S1–S6). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Bao et al., 2013; Mei et al., 2015; Mesik et al., 2013). For each comparison, Cohen's *d* was used to compute the effect size (Cohen, 1992).

2.3. Results

During adaptation to point-light walkers with leftward or rightward facing directions, the percentage of points of the adapting facing direction involved in the chimeric ambiguous walkers (test stimuli) increased significantly ($t(11) = 8.39$, $p < 0.001$, $d = 2.42$), showing a clear adaptation aftereffect ($M = 14.8 \pm 6.1\%$, see Fig. 3). By contrast, the position-scrambled adapters failed to induce a significant aftereffect ($t(11) = -0.19$, $p > 0.25$, $d = 0.05$) (see Fig. 3). During the "deadaptation" period in the PLW adapting condition, the adaptation effects quickly decayed to the baseline levels (deadaptation duration: 68.3 ± 14.3 s).

More important, the linear trend analysis showed a strong spontaneous recovery in the post-tests for the PLW adapting condition (see Fig. 3, $t(11) = 5.37$, $p < 0.001$, $d = 1.55$). The recovery rapidly reached the highest level at approximately the 68-s point (peak time) in the initial phase of the post-test period. Then the adaptation effect decayed slowly and remained above the baseline until the end of the post-test period ($p < 0.05$ for all time points). These results, for the first time, indicated that biological motion adaptation was controlled by multiple mechanisms. In the position-scrambled condition, the adaptation effects at the first two time points (but not thereafter) of the post-test were below the baseline ($p < 0.05$, see Fig. 3). To examine any spontaneous recovery in this control condition, we also conducted the linear trend analysis. However, the results did not reach statistical significance ($t(11) = 1.32$, $p > 0.20$, $d = 0.38$).

There was an initial drop on the time course of the adaptation effect after the deadaptation in the scrambled adaptation condition in Experiment 1 (see Fig. 3). We speculate that the termination rule of the deadaptation period could lead to the initial drop. According to the termination rule, deadaptation was terminated whenever the adaptation effect (i.e. the percentage of points in the adapting direction of the chimeric test stimulus) was lower than the baseline. Given that the adaptation effect was negligible in the scrambled condition, a response causing the staircase to descend for one step (or test level) would be sufficient to trigger the termination of the deadaptation. This occurred in every session in the scrambled condition. However, the adaptation effect in the PLW adapting condition was often profound and sometimes remained above the baseline by the end of deadaptation. Therefore, after averaging across the sessions for each subject, the adaptation effect by the end of deadaptation was always below the baseline in the scrambled condition but varied around the baseline in the PLW adapting condition.

3. Experiment 2

3.1. Methods

3.1.1. Participants

Twelve subjects (seven females, 20–26 years old, mean age = 21.6 years, SD = 1.6) participated in Experiment 2. Five of them had participated in Experiment 1.

3.1.2. Apparatus and stimuli

The same apparatus and stimuli were used as in Experiment 1, except that position-scrambled adapters were excluded.

3.1.3. Procedure

The same procedures as in Experiment 1 were used except the followings. There were three stages of each session in Experiment 2 (see Fig. 2B): a "baseline" period, an "adaptation" period and a "post-test" period. The deadaptation stage was removed, and the "post-test" period was extended to 300 s (150 trials). In addition, adaptation durations of 182 s (26 trials), 301 s (43 trials) and 420 s (60 trials) in the "adaptation" period were used across sessions. For each of the adaptation durations, subjects finished twelve sessions, with six sessions for each facing direction (leftward or rightward) of the PLW adapters.

3.2. Analysis

The estimation of the baseline and the normalization, and interpolation analysis were the same as in Experiment 1. Because adaptation effects kept growing near the end of initial adaptation period under the two shorter adaptation duration conditions (see Fig. 4), here we used the percentage of points of the last 3 reversals of the test stimuli to compute the adaptation effects. A One-Way Repeated Measure ANOVA was performed to evaluate the effect of adaptation duration on adaptation aftereffects. Moreover, we used Vul et al.'s (2008) method to estimate the slow and fast timescales of adaptation effects. The magnitude of the slow timescale was defined as residual adaptation effects at the last 20 s of the post-test period; the magnitude of the fast timescale was defined as the difference between adaptation effects in the adaptation period and residual adaptation effects in the post-test period. Then a One-Way Repeated Measures ANOVA was performed to compare the magnitude of the slow and fast timescale adaptation under the three adaptation duration conditions. For each ANOVA test, Eta-squared (η^2, sums of squares for the effect of interest divided by the total sums of squares) was used as estimate of the effect size (Cohen, 1973).

3.3. Results

The time courses of build-up and decay of biological motion adaptation were shown in Fig. 4 for three adaptation durations. There were significant adaptation effects for all the three adaptation duration conditions (see Fig. 4, 182-s duration: $M = 13.0\% \pm 4.9\%$, *t*

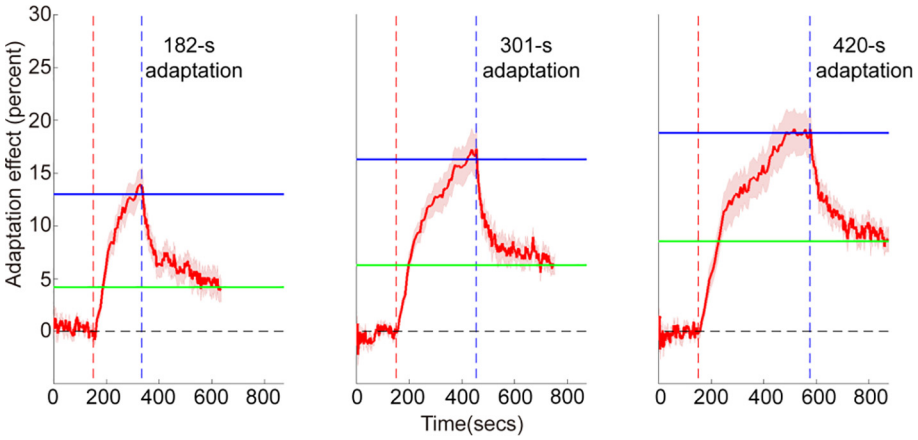

Fig. 4. Grand average time courses for the three adaptation durations in Experiment 2. Plotting conventions are same as in Fig. 3, except the followings. The two vertical lines mark the onsets for the adaptation and decay periods respectively, and the horizontal blue and green lines represent adaptation effects and residual adaptation effects, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(11) = 9.22, $p < 0.001$, $d = 2.66$; 301-s duration: $M = 16.3\% \pm 6.2\%$, $t(11) = 9.08$, $p < 0.001$, $d = 2.62$; 420-s duration: $M = 18.8\% \pm 6.8\%$, $t(11) = 9.58$, $p < 0.001$, $d = 2.77$). A One-Way Repeated Measures ANOVA showed that the adaptation duration had a significant effect on the aftereffect magnitude ($F_{(2, 22)} = 15.17$, $p < 0.001$, $\eta^2 = 0.64$). The *post-hoc* paired comparison *t*-tests with Bonferroni correction showed that adaptation effects became stronger as adaptation durations grew ($p < 0.05$ for all three comparisons).

An inspection of the post-test period in Fig. 4 found that adaptation effects decreased rapidly at the initial phase but then decayed slowly, suggesting that there were likely two timescales involved in the adaptation. Comparing to a single exponential model, the two-timescale linear model developed by Vul et al. (2008) provided a better fit to our data (see Figs. S7 and S8 in the Supplementary Materials). Specially, the two-timescale linear model accounted for 96%, 98% and 97% of the total variance of the data for the 182-s, 301-s and 420-s duration conditions, respectively; however, the single exponential model only accounted for 77%, 64% and 76% of the total variance of the data for the three conditions. Considering that more free parameters were involved in the two-timescale linear model than in the single exponential model, Akaike's information criterion (AIC) test was performed to deal with the model selection. The AIC values for the two-timescale linear model were −1854.92, −2047.67 and −2110.55 for the 182-s, 301-s and 420-s duration conditions, respectively, which were lower than the AIC values for the single exponential model (−1412.05, −1316.58 and −1351.93 for the 182-s, 301-s and 420-s duration conditions, respectively). According to the decision rule of the AIC, the model with the minimum AIC value is considered to be the preferred model. Therefore, the two-timescale linear model was superior to the single exponential model.

To perform the comparisons statistically, we used the Vul et al. (2008)' method to separate the slow and fast timescales of adaptation effects (see Analysis above). One-Way Repeated Measures ANOVAs revealed that adaptation duration had a significant effect on the slow timescale (see Fig. 5, $F_{(2, 22)} = 11.93$, $p < 0.001$, $\eta^2 = 0.52$) but not on the fast timescale (see Fig. 5, $F_{(2, 22)} = 1.79$, $p > 0.05$, $\eta^2 = 0.14$)(see the results in Tables 1 and 2 of Supplementary Materials when using different reversals of the test stimuli near the end of the adaptation period to compute adaptation effects). The *post-hoc* paired comparisons showed that the residual adaptation effects of the 420-s duration condition were significantly stronger than that of the 182-s and the 301 duration condition ($p < 0.05$ for the two comparisons). Although the residual adaptation effects of the 301-s duration condition were larger in magnitude than that of the 182-s duration condition, the difference of both did not reach a statistical significance ($p = 0.15$). These results suggested that the slow component of the adaptation effects was longer-lasting as adaptation duration increased. Taken together, the dynamics of biological motion adaptation also obeyed the duration scaling law.

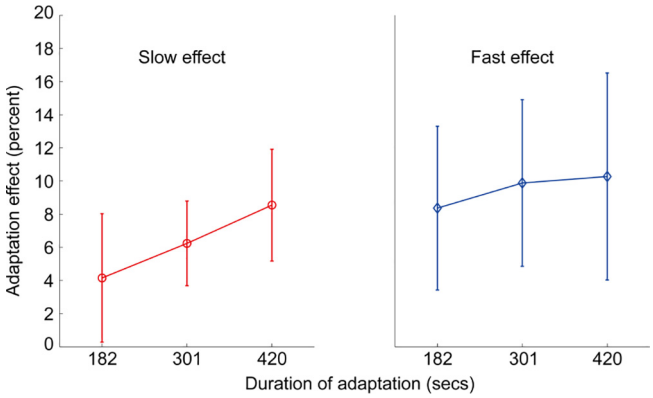

Fig. 5. The magnitude of adaptation of the slow (left panel) and fast (right panel) timescales as a function of adaptation durations in Experiment 2. Error bars show ± one standard error of the mean across subjects. The slow effect, but not the fast effect, becomes stronger as adaptation duration grows.

This is in line with other adaptation phenomena such as McCollough effect (Vul et al., 2008) and effects of contrast adaptation (Bao & Engel, 2012; Greenlee et al., 1991).

4. Discussion

Using the top-up paradigm and the deadaptation procedure, in Experiment 1 we observed the spontaneous recovery of adaptation effects in biological motion perception. Similar phenomenon has been found in motor adaptation (Smith, Ghazizadeh, & Shadmehr, 2006), McCollough effect (Vul et al., 2008), contrast adaptation (Bao & Engel, 2012; Bao et al., 2013), motion and face adaptation (Mesik et al., 2013). The reasonable interpretation is that a "slow" and a "fast" mechanism corresponds to engage relatively long adaptation and short deadaptation, respectively. Because deadaptation, mainly controlled by the fast mechanism, can only temporarily cancel (or mask) the longer-lasting adaptation effects that are controlled by the slow mechanism, the spontaneous recovery emerged in the initial phase of the post-test period. Our findings for the first time disclose that this notion of multiple temporally-tuned mechanisms can account for the temporal dynamics of biological motion adaptation.

When using the deadaptation paradigm, the present study confronted the same limitation as the previous work (Kwas, 1999; Magnussen & Greenlee, 1986; Mesik et al., 2013): adaptation mechanisms relating to the specific adapters in the adaptation and the deadaptation stage could explain spontaneous recovery. Take the current experiment as an example. A leftward and a rightward PLW adapter could be encoded by the two groups of neurons. Different adapting durations could engender differential decay rates of

adaptation in these two groups of neurons, which resulted in the spontaneous recovery in the post-test period. Therefore, although multiple temporally-tuned mechanisms are suggested to explain the spontaneous recovery observed in the current study, the phenomenon can also be explained by two adapter-specific mechanisms tuned to opposite facing directions. Using the stimuli in the present study, we could not rule out this latter explanation. Whether biological motion adaptation is controlled by multiple temporally-tuned or contextually-tuned mechanisms remained to be explored in future work.

The current results showed that adaptation to a leftward or a rightward direction of limited lifetime PLW produced the opposite perception of biological motion to ambiguous test stimuli, replicating the findings in a previous study using the similar adapters and test stimuli (Theusner et al., 2011). However, that study adopted the method of constant stimuli rather than the staircase procedure to measure the adaptation effects. Therefore, Theusner et al. (2011) cannot examine the time course of biological motion adaptation. For the first time, our work investigated the time course of biological motion adaptation, and revealed that the duration scaling law held in this type of adaptation. Moreover, the results of Experiment 2 showed that the slow component of the adaptation effects became stronger as adaptation durations increased, a result consistent with a previous study of McCollough effect (Vul et al., 2008). In Vul et al.'s study, the fast component of the adaptation effects saturated under the 160-s adaptation duration condition but not under the 40-s adaptation duration condition. In the present study, the fast component showed no significant difference among the 182-s, 301-s and 420-s adaptation duration conditions. Given that shorter adaptation durations were not used for the adapter stimuli in the current study, further research will be required to examine how long it would take for the fast component of biological motion adaptation to reach asymptote.

In conclusion, using the limited-life point-light walkers, we observed spontaneous recovery of effects of biological motion adaptation and showed that the effects of biological motion adaptation complied with the duration scaling law. The present work suggests that this type of visual adaptation was likely controlled by multiple temporally-tuned mechanisms. These findings, taken together with the past studies, indicate that multiple adaptation mechanisms appear to be a universal principle in visual adaptation.

Author contributions

MB conceived the study, GM and YP designed the study, QY and GL conducted the experiments, GM performed data analysis, GM and MB wrote the paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2018.06.001.

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