

Illusory Motion of the Motion Aftereffect Induces Postural Sway

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Since the pioneering work of David Lee and his colleagues (Lee & Aronson, 1974; Lishman & Lee, 1973), the significant role that visual stimulation plays in postural control has been well established. For instance, visual stimuli simulating self-motion through the environment generate potent postural adjustments in observers (Bronstein & Buckwell, 1997; Guerraz & Bronstein, 2008; Lestienne, Soechting, & Berthoz, 1977; Meyer, Shao, White, Hopkins, & Robotham, 2013; van Asten, Gielen, & van der Gon, 1988). In all the studies just cited, the postural adjustments occurred as a result of motion information in a visual stimulus that was presented to the observer (i.e., direct visual stimulation).

It remains an open question, however, whether this perception-action cycle is the result of direct visual stimulation only, or whether postural adjustments also occur when the motion of the visual stimulus is illusory. Here, we show that the latter is the case. Prolonged viewing of visual motion results in neural adaptation, and subsequent viewing of a stationary stimulus normally results in illusory motion in the opposite direction, a famous phenomenon known as the motion aftereffect (MAE; Anstis, Verstraten, & Mather, 1998). Surprisingly, this sequence of stimulation also causes postural sway in the direction consistent with the perceived illusory motion. Control test patterns that do not generate an MAE after identical adaptation do not induce sway. This suggests that the visuo-vestibular interactions that govern postural control are not influenced by visual stimulation per se, but can be modulated by an illusory motion signal (e.g., the internal neural signal responsible for the MAE).

Different Test Patterns Cause Different Postural Sway

Visual experience is often the direct result of visual stimulation. Hence, it is not surprising that most research on visuo-vestibular interactions has used direct visual stimulation, such as optic-flow stimuli simulating self-motion

(Masson, Mestre, & Pailhous, 1995; Stoffregen, 1986). To be able to disentangle actual (direct) visual stimulation from visual experience, we used the MAE. During our experiment, observers ($N = 7$) stood in a completely dark room on a force plate (Fig. 1a). The recorded posturographic data were used to analyze the center-of-pressure (COP) displacement in the medial-lateral direction. Observers stood in front of a projection screen ($87^\circ \times 56^\circ$) and visually adapted to a binary random-pixel array (RPA; 50% dark pixels, 50% bright pixels) that was translating leftward or rightward with a speed of approximately $3^\circ/\text{s}$. The RPA was initially presented for 40 s to build up adaptation; 20-s top-up adaptation epochs were used between trials to keep observers maximally adapted. Each adaptation epoch was followed by a black screen for 2 s and then a 14-s presentation of the test pattern. Observers had to press a button to report when the MAE dissipated, if its duration was shorter than 14 s.

Three different test patterns were used: a static version of the RPA, a dynamic version of the RPA in which each pixel was randomly assigned a dark or bright polarity every 16.7 ms (Verstraten, van der Smagt, & van de Grind, 1998), and a black screen. The dynamic test pattern was expected to generate a shorter MAE than the static test pattern, as previous results have shown that following adaptation to low-speed moving stimuli, longer MAEs are induced by static test patterns compared with dynamic test patterns (Verstraten et al., 1998). The black screen served as a control condition that was expected not to induce an MAE, because no reference cues were present on the screen. Therefore, any postural sway induced by this black test pattern could be considered to be the result of postural compensation. (For additional information on the experimental method, including data analysis, see Methodological Details in the Supplemental Material available online.)

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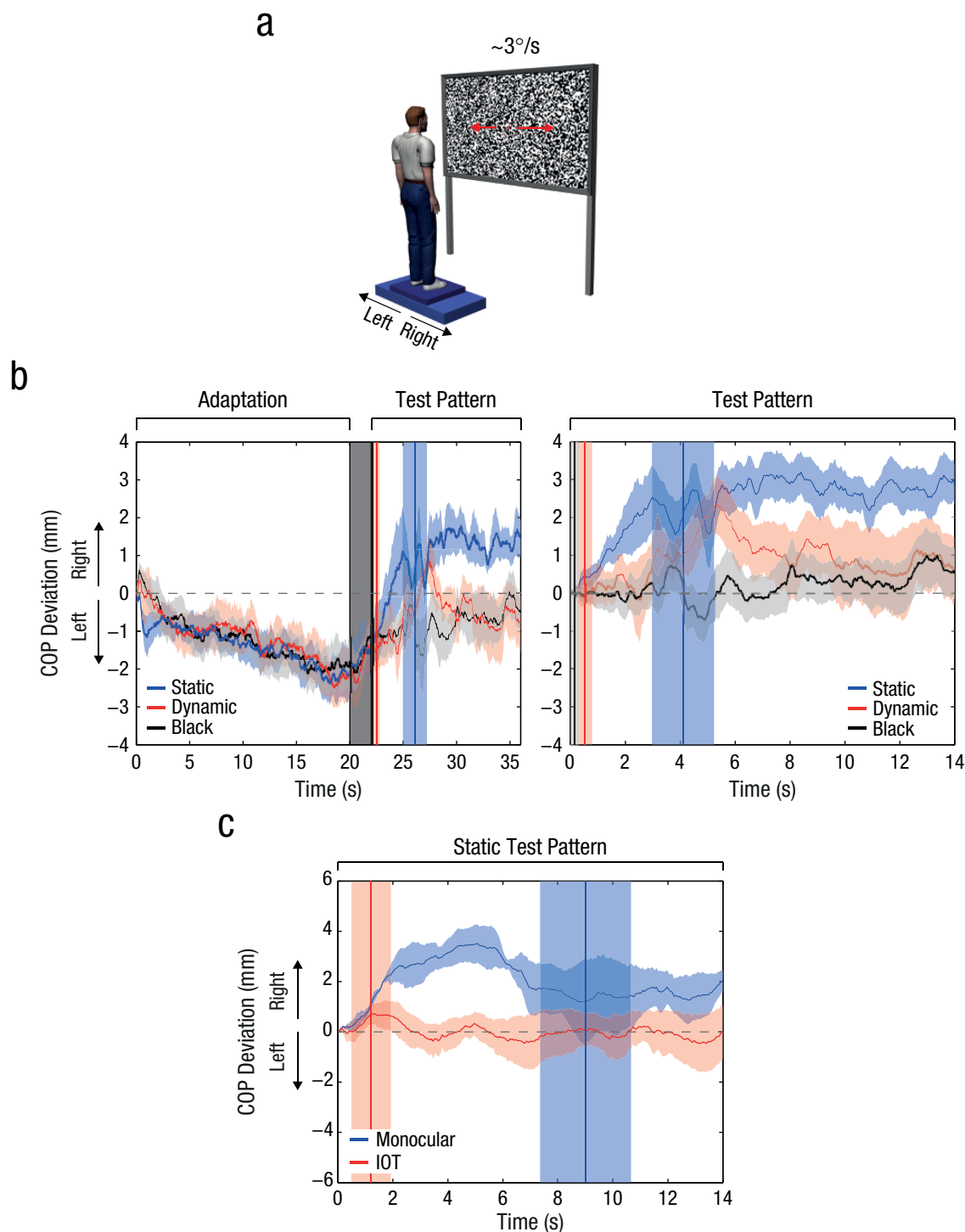


Fig. 1. Illustration of the experimental setup and experimental results. During the main experiment, observers stood on a force plate and viewed a projection screen (a). They visually adapted to a binary random-pixel array (50% dark pixels, 50% bright pixels) that was translating leftward or rightward at a rate of approximately 3°/s. Each adaptation epoch was followed by a black screen and then a presentation of the test pattern. The recorded posturographic data were used to analyze the center-of-pressure (COP) displacement in the medial-lateral direction. The graphs in (b) show COP deviation and reported offset of the motion aftereffect (MAE; vertical bars) for the three test patterns (static, dynamic, black) used in the main experiment. The left graph shows results averaged across observers ($N = 7$) over the time course of a trial. The dark-gray region between 20 and 22 s after stimulus onset indicates the black screen that was presented between the adaptation and test patterns in all conditions. The right graph shows results averaged across observers with the COP at the start of the test pattern serving as baseline. Note that the time scale is changed, so that Time 0 is the onset of the test pattern. The graph in (c) shows COP deviations and corresponding MAE offsets (vertical bars) from the monocular and interocular-transfer (IOT) conditions in the supplemental experiment. Results are averaged across observers ($N = 3$) with the COP at the start of the test pattern serving as baseline (again, Time 0 is the onset of the test pattern). In all the graphs, results for the two motion directions are collapsed, with all trials converted to leftward adaptation. The bold lines indicate averages across observers, and the light shaded regions represent ± 1 SEM.

The reported MAE duration and the amount of postural sway averaged across observers are depicted in Figure 1b. During adaptation, the observed postural sway was in the same direction as the motion direction of the stimulus; this result corroborates previous findings (Bronstein, 1986; Holten, Donker, Verstraten, & van der Smagt, 2013; Lestienne et al., 1977). After the adaptation stimulus was replaced by a black test pattern, the COP gradually returned to baseline (i.e., the COP at the start of the trial). Observers did not report an MAE in most of these trials (94%). As expected, the static test pattern induced an MAE that was significantly longer than the one induced by a dynamic test pattern, $t(6) = 3.34$, $p = .047$, $r = .81$. Moreover, the static test pattern caused the COP to move beyond baseline in the direction opposite that observed during adaptation.

In accordance with the MAE durations observed, the dynamic test pattern appeared to generate less postural sway than the static test pattern. To compare the amount of postural sway generated by the test patterns, we set the COP at the start of the test pattern to zero and calculated the area under the curve of each test pattern (mean integral; static test pattern: 32.9; dynamic test pattern: 12.4; black screen: 2.8; see Fig. 1b, and Fig. S1 in the Supplemental Material). A repeated measures analysis of variance demonstrated a main effect of test-pattern type on the amount of postural sway, $F(2, 12) = 6.99$, $p = .010$, $\eta_p^2 = .54$. Post hoc pairwise comparisons showed that more postural sway was generated by the static than by the black test pattern ($p = .019$). The static test pattern also generated a longer MAE than the black test pattern did, $t(6) = 4.00$, $p = .021$, $r = .85$. The results therefore show that after identical adaptation, the type of test pattern affects the amount of postural sway and the perceived strength (duration) of the MAE in a similar fashion.

Interocular Transfer of the MAE and Postural Sway

Further evidence that the illusory experience of visual motion influences postural sway comes from a supplemental experiment in which we used interocular transfer (IOT) of the MAE. The method of this experiment was largely identical to that of the main experiment, except that adaptation to the translating RPA was monocular and the following static test pattern was presented to either the same, adapted, eye (monocular condition) or the other eye (IOT condition). (For details of the methodological differences between the two experiments, see Methodological Details in the Supplemental Material.) IOT of the MAE is suboptimal, and therefore the duration of the MAE is shorter in the IOT condition compared with the monocular condition (Wade, Swanston, & de Weert, 1993). If postural sway is related to the experience of visual motion rather than to the veridical sensory input

itself, less postural sway should be induced in the IOT condition than in the monocular condition. As expected, the duration of the MAE was shorter in the IOT condition than in the monocular condition, and there was also less postural sway in the IOT condition, $t(2) = -4.869$, $p = .040$, $r = .96$ (Fig. 1c). These results indicate that the illusory motion of the MAE, and not merely postural compensation and recalibration, caused the postural sway during the presentation of the static test pattern.

Conclusion

Our results are relevant to the as-yet-unresolved discussion on whether perception is *indirect* or *direct* (i.e., whether perception is top-down and inferential or whether it is exclusively derived from afferent retinal information; Wertheim, 1994). Our results show that the neural motion signal from the MAE influences the perception-action cycle. Therefore, it seems that it is not the veridical sensory input itself but rather the integration of sensory information and perhaps prior expectations that drive postural sway. This would be in line with predictive processing in which the brain matches prior top-down expectations and predictions with incoming sensory inputs (Clark, 2013). All in all, the visuo-vestibular interactions involved in visual-motion-induced sway seem to be influenced by the actual experience of visual motion, rather than visual stimulation per se.

Author Contributions

All the authors contributed to the study design. Data collection and data analysis were performed by V. Holten. All the authors contributed to the interpretation of the data. V. Holten drafted the manuscript, and M. J. van der Smagt, S. F. Donker, and F. A. J. Verstraten provided critical revisions. All the authors approved the final version of the manuscript for submission.

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.

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Supplemental Material

Additional supporting information can be found at <http://pss.sagepub.com/content/by/supplemental-data>

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Supplemental Methodological Details

Main experiment

Observers

Eleven observers (age between 19-26 years) participated in the experiment of which four had to be excluded from the analysis since they became dizzy during the experiment and had to stop. All observers had normal or corrected-to-normal visual acuity. We selected the number of observers based on the amount of participants that previous psychophysical (motion aftereffect) studies have used. The experiment involved healthy human participants, and did not utilize any invasive techniques, substance administration or psychological manipulations. Therefore, compliant with Dutch law, this study only required, and received approval from our internal faculty board (Faculty's Advisory Committee under the Medical Research Human Subjects Act, WMO Advisory Committee) at Utrecht University. Written informed consent was obtained from all observers. The experiment was conducted according to the principles expressed in the Declaration of Helsinki. By signing the informed consent, observers indicated to have read and agreed with both the rules regarding participation and proper (laboratory) behavior, and the researchers' commitments and privacy policy. Observers were also informed that they could stop participating in the experiment at any time and that all data would be analyzed anonymously.

Stimuli & Apparatus

Stimuli were generated on a MacPro and projected on a flat rear projection screen (87° x 56°, 220 x 124.5 cm) by a DepthQ HDs3D-1 projector (refresh rate 60Hz, resolution 848 x 480 pixels). Each pixel of the random-pixel-array (RPA) corresponded to one pixel on the projector grid. The color (black/white) of each pixel was randomly assigned. Pixels of the RPA that reached the border of the screen were randomly refreshed and replaced at the other side of the RPA. Posturographic data of observers was measured using a custom-made forceplate (ForceLink BV, sample frequency 1000Hz).

Procedure

Observers stood on a forceplate covered with foam and viewed the projection screen from a distance of 116cm. They were asked to stand with their feet approximately shoulder width apart, keep their weight equally distributed between their feet and hold their arms at their sides. The adaptation stimulus contained a fixation dot (diameter 0.20 degrees). When no fixation dot was present, observers were asked to fixate on the center of the screen. The adaptation stimuli were presented in blocks (7 blocks leftward motion, 7 blocks rightward motion) and within a block each test pattern was presented 3 times. Blocks, as well as the test patterns within a block were presented in pseudo-random order. Each of the 6 (3 test patterns * 2 adaptation directions) conditions was presented 21 times, resulting in 126 trials in total. Between blocks (~ 5.8 min) observers could take a break.

Analysis

After down-sampling the data from the forceplate to 125 Hz, the center of pressure (COP) in the medial-lateral direction was calculated. To remove measurement noise, the COP data was filtered with a 4th-order Butterworth filter (cutoff frequency 10 Hz).

Statistics

The data of the two motion directions was collapsed, with all trials converted to leftward adaptation. A repeated measures analysis of variance (ANOVA) was performed on the area under the curve for all observers for each test pattern type (3 levels: static, dynamic, black). Pairwise comparisons with a Sidak correction were used to examine significant differences between conditions. Paired sample *t*-tests with Bonferroni correction were used to compare the median motion aftereffect duration of all observers for each test pattern type.

To compare the postural sway induced by the static or dynamic test pattern with the sway resulting from postural compensation (black test pattern), difference scores between the COP deviation of the static - black and the dynamic - black test pattern were calculated. For each time sample (8ms), the difference score was compared

with zero using t -tests ($\alpha = 0.025$). When at least 25 consecutive time samples (200ms) were significantly different from zero, the postural sway within that time interval was considered to be significantly different from postural compensation. Figure S1 shows the postural sway induced by the three test patterns and the time intervals where the deviation between the static - black and dynamic - black test pattern were significantly different from zero. The sway induced by the static test pattern is significant from postural compensation for a much longer period of time than the sway caused by the dynamic test pattern.

Additional experiment

The methods of the additional experiment are identical to the main experiment except for the specific differences mentioned below.

The MAE duration and the amount of postural sway was measured for 3 observers of which one author. We decided to use 3 observers, since the experiment required experienced observers and was an addition to the first experiment. At the start of each trial, each observer had to adapt for 40s to a leftward moving random-pixel-array, presented to the right eye only. Each adaptation epoch was followed by a 2s black screen, subsequently replaced by a static version of the random-pixel-array that was randomly presented either to the left (IOT condition) or to the right eye (monocular condition). In total, the static test pattern was presented 20 times to each eye. Observers viewed the projection screen through shutter-glasses (PLATO visual occlusion spectacles, Translucent Technologies) and the eye that was not supposed to view the adaptation or the test pattern was occluded.