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Static and dynamic visual cues in feed-forward postural control

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Abstract

Anticipatory postural adjustments (APAs) play an important role in the performance of many activities requiring the maintenance of vertical posture. However, little is known about how variation in the available visual information affects generation of APAs. The purpose of this study was to investigate the role of different visual cues on APAs. Ten healthy young subjects were exposed to external perturbations induced at the shoulder level in standing while the level of visual information about the forthcoming perturbation was varied. The external perturbations were provided by an aluminum pendulum attached to the ceiling. The visual conditions were (1) dynamic cues (full vision and high-frequency strobe light), (2) static cues (low-frequency strobe light) and (3) no cues (eyes open in dark room). Electrical activity of the trunk and leg muscles and center of pressure displacements were recorded and quantified within the time intervals typical for APAs. The results showed that significantly larger APAs were generated in conditions with dynamic visual cues as compared to the conditions with static cues ($p < 0.05$). Finally, no APAs were observed in the condition where there was complete absence of any visual cues. Principal component analysis further revealed different muscle coupling patterns in the full vision and high-frequency strobe light conditions. These findings suggest the importance of using appropriate visual cues in the generation of APAs.

Keywords

Posture; Feed-forward; Visual cues

Introduction

Upright stance in humans is controlled by multisensory interactions of the visual, somatosensory and vestibular systems (Winter 2000). While the contribution of somatosensory and vestibular systems to postural control is well documented in the literature, the role of the visual system in control of balance is less understood, despite its importance (Wade and Jones 1997). This could be because the obtaining and processing of visual information is affected by many factors within human beings themselves, the environment and the interaction between the two. For example, visual acuity, contrast sensitivity and depth perception play a significant role in how humans themselves can see the object with clarity. Environmental factors such as lighting in the room also affect the way the individuals see the surrounding. For example, previous literature has shown humans demonstrate diminished ability to control posture in conditions with dimmed lights (Owsley and Sloane 1987; Lord and Menz 2000).

When humans maintain vertical posture, the central nervous system (CNS) uses two types of adjustments in the activity of the trunk and leg muscles. The first one, anticipatory (feed-forward) postural adjustments (APAs) (Massion 1992) are associated with the activation of muscles prior to the actual perturbation of balance. The assumed role of APAs is to minimize the negative consequences of a predicted postural perturbation (Bouisset and Zattara 1987; Massion 1992). The second type of adjustment in the activity of postural muscles is the compensatory (feedback) reaction that deals with actual perturbations of balance compensating for the suboptimal efficacy of APAs; these reactions are initiated by sensory feedback signals (Park et al. 2004; Alexandrov et al. 2005). It was shown that the presence of strong APAs increases postural stability (Santos et al. 2010b; Santos et al. 2010a) and that vision plays an important role in generation of APAs (Krishnan and Aruin 2011; Mohapatra et al. 2011). In particular, APAs associated with catching a load were seen when the subjects watched the upcoming object, but they were absent when the eyes of the subjects were closed (Lacquaniti and Maioli 1989). Similar results were obtained in a series of experiments involving external perturbations induced by a pendulum impact (Santos et al. 2010a). Furthermore, when healthy subjects were catching a falling load onto a tray attached to their trunk and were able to see the load during the first 10 cm of its trajectory (which was approximately 140 ms after the object was released by an experimenter), APAs timed appropriately with respect to the moment of load impact were generated (Aruin et al. 2001). Overall, the outcomes of the previous studies suggest that when adequate visual information for an accurate prediction of the impact time is available, strong APAs can be generated. At the same time, it was shown that diminished visual acuity (induced by differently powered glasses) affected the ability of subjects to predict the impending external perturbation and as such the generation of APAs (Mohapatra et al. 2011). While the previous studies provided important information on the role of vision in the control of posture using anticipatory postural adjustments, in most of the cases they did not study the effect of different visual cues upon APAs.

Visual cues can be described using two main classifications. The first one is based on the way the cues are obtained, either with one or two eyes (monocular or binocular cues). The second classification described in the literature is based on the duration of visual information (static cues and dynamic cues). When an object is visible throughout the whole length of time it is moving (this can only be possible when the subject has full vision and can see the object during its whole path), the visual information is obtained using dynamic visual cues. The spatiotemporal relation between the subject and surrounding environmental objects is thus provided by dynamic information from the retina that is mainly generated by the observer's self motion (Sun et al. 2004) as well as the motion of the objects in the environment (Sun and Frost 1998). When the individual is able to see the object at specific intervals of time but not through the entire length of time, the visual information is obtained via static visual cues. For example, static cues are available when in a dark environment a light exposes the object for a fraction of a second. It is important to note that when the frequency of light on the object is low, visual information about the movement of the object is inaccurate. At the same time, when the frequency of light on the object increases, the visual information becomes more accurate (Bull et al. 2003).

Visual cue-related differences in processing information could affect the movement performance. Previous studies reported that goal-directed movements are affected by visual cues (Greenwald et al. 2005). For example, when vision is compromised or not available, a person might experience additional challenges when reaching for an object or walking. Thus, understanding motor control issues related to the use of visual information is important.

Visual cues are also important for maintaining vertical posture which becomes even more important in the presence of external perturbations. In such a case, precise visual information about the approaching object could significantly increase the efficacy of postural control. However, the extent to which available visual information about the impending perturbation affects the control of posture has not been fully investigated. In particular, it is not known how different visual cues are utilized in generation of APAs. Thus, the aim of the current study was to investigate the role of static and dynamic visual cues in the generation of the anticipatory postural adjustments. We hypothesized that when healthy subjects are provided with static visual cues about the forthcoming perturbation, they will demonstrate diminished ability to generate anticipatory postural adjustments as compared to conditions where they are provided with dynamic visual cues. To test the hypothesis, we utilized a pendulum paradigm to induce external body perturbations of the same magnitude while the level of visual information about the forthcoming perturbation was varied.

Methods

Subjects

Ten healthy young subjects (6 females and 4 males, mean age of 26.8 ± 1 years, a mean weight of 65.7 ± 4.6 kg and height of 1.67 ± 0.3 m) participated in the study. All of the study participants had 6/6 visual acuity; they had no musculoskeletal, neurological or balance disorders. The subjects signed an informed consent approved by the Institution Review Board.

Procedure

The subjects were positioned on a force platform (Model OR-5, AMTI, USA) facing an aluminum pendulum attached to a ceiling that was used to induce body perturbations after being released by the experimenter. The pendulum design allowed perturbations to be induced in the sagittal plane, and the perturbations were applied to the body at the shoulder level (Fig. 1). The subjects stood barefoot with their feet shoulder width apart and hands by their sides. More details about the pendulum paradigm can be found in our previous publications (Krishnan and Aruin 2011; Mohapatra et al. 2012). The perturbations of the same magnitude were induced in conditions with different availability of visual cues. The experimental conditions were dynamic visual cues: full vision (FV) and high-frequency (66.67 Hz) strobe light condition (HFS); static cues: low-frequency (5.83 Hz) strobe light condition (LFS); and a control condition: no cues provided at all. In the later case, the subjects' eyes were open while the room was completely dark (EOD). The strobe light was flashed on the pendulum by a Stroboscope (Model: GenRad1531-AB STROBOTAC) and was turned on a few seconds before the pendulum release, while keeping it on during data collection. The lengths of light and dark phases were of equal durations for a particular frequency. Thus, the duration for which the flash was either on or off for HFS condition was about 8.5 ms, whereas for LFS it was about 85 ms. The intensity of the flash was about 0.16 million beam candles for LFS and 1 million beam candles for HFS. The subjects were always instructed to keep their eyes open and look at the oncoming pendulum. In the EOD condition, the room was made completely dark and the experimenter ensured that the subject did not see the pendulum while keeping their eyes open. In all the conditions, the time the pendulum moved from the moment of its release till perturbing the body was the same. However, the subject was able to see the pendulum during its path more frequently in HFS than in LFS. The subjects wore wireless headphones playing music in all of the conditions, so any kind of auditory information which would have alerted them about the moment of release of the pendulum was blocked. Each subject was given a couple of practice trials

prior to administering actual recording of three trials in each experimental condition. The order of experimental conditions was randomized.

Instrumentation

A 16-channel portable EMG unit (RUN Technologies, USA) was used to record electrical activity of the following nine muscles on the right side of the body: tibialis anterior (TA), semitendinosus (ST), medial gastrocnemius (MG), biceps femoris (BF), rectus femoris (RF), gluteus medius (GM), external oblique (EO), rectus abdominis (RA) and erector spinae (ES). After the skin area was cleaned with alcohol wipes, disposable surface electrodes (Red Dot 3 M) were attached to the muscle belly of each of the abovementioned muscles based on recommendations reported in the literature (Basmajian 1980). The distance between the electrodes of a pair was about 4 cm. After similar skin preparations, a ground electrode was attached to the anterior aspect of the leg over the tibial bone. The EMG signals were collected, filtered and amplified (10–500 Hz, gain 2000).

An accelerometer (Model 208CO3, PCB Piezotronics Inc., USA) was attached to the participant's left clavicle to record time of impact of the pendulum. Ground reaction forces and moments in the X, Y and Z planes were recorded by the force platform (AMTI, USA). The forces, moments of forces, EMG and accelerometer signals were digitized with a 16-bit resolution at 1,000 Hz and recorded by a customized LabVIEW 8.6.1 software (National Instruments, Austin, TX, USA).

Data processing

All signals were processed offline using customized MATLAB 7.13 software (Math Works, Natick, MA, USA). First, EMG signals were rectified and filtered with a 50-Hz low-pass, second-order, zero-lag Butterworth filter, while the ground reaction forces and moments were filtered with a 20-Hz low-pass, second-order, zero-lag Butterworth filter. Second, the accelerometer signal was corrected for offset. “Time-zero” ($T_0 = 0$, the moment of pendulum impact) acquired by a computer algorithm was set as a point in time at which the signal exceeded 5 % of the maximum. An experienced researcher confirmed this value by a visual inspection. Then, all trials were aligned to T_0 and integrals of EMGs, muscle latencies and CoP displacements were calculated. In order to do this, the data for further analysis were selected in the range from –1,000 ms (before T_0) to +500 ms (after T_0), out of which –1,000 to –850 ms of the data were taken for baseline activity. The averaged EMG signals for each muscle for each subject were integrated with 150 ms time windows for two time windows representing the –250 to +50 ms of the data. Each of the time windows was further corrected by the averaged 150 ms baseline activity. Then, the integrals of EMG for each muscle for each subject were normalized to the maximum integral magnitude across all the conditions. The outcome of the normalization will be denoted as $IEMG_{NORM}$.

Due to the normalization, all of the $IEMG_{NORM}$ values were within the range from +1 to –1 (Krishnan and Aruin 2011). Two, 150-ms duration epochs were selected in relation to T_0 : (1) from –250 to –100 ms (anticipatory, APA1) and (2) from –100 to +50 ms (anticipatory, APA2) (Santos et al. 2010a, b). The division of the APA interval into two epochs would allow examining changes in the anticipatory EMG activity more precisely.

A time window from –250 to +250 ms in relation to T_0 was utilized to detect muscle latencies by the combination of both a computer algorithm and a visual inspection of the individual traces for each muscle. The latency for a specific muscle was defined as the instant when its EMG amplitude was greater (activation) or smaller (inhibition) than the mean ± 2 SD of the baseline (–500 to –400 ms with respect to T_0), lasting for at least 50 ms. PCA was applied to correlation matrices of muscles latencies data of all the subjects. The

PCs were further subjected to Oblimin with Kaiser Normalization rotation with factor extraction.

Time-varying CoP displacement was calculated using the approximation described in the literature (Winter et al. 1996). CoP displacements were calculated only in the anterior–posterior direction due to the symmetrical nature of the perturbation. The CoP signals were corrected by their respective baseline, and the CoP data windows were shifted 50 ms forward to account for the electro-mechanical delay (Cavanagh and Komi 1979; Howatson et al. 2009). The magnitude of CoP at the moment of perturbation (T_0) and the peak magnitudes of the CoP were calculated.

Statistical analysis

Repeated-measures ANOVAs were performed with two within-subject factors: conditions (FV, HFS, LFS, and EOD) and epochs (APA1 and APA2). The dependent variables were IEMG_{NORMS}, latency of trunk and leg muscles, magnitude of CoP at the moment of perturbation (T_0), and peak magnitude of the CoP.

Further comparisons between conditions, epochs and their interactions were done by a post hoc analysis using a pair-wise *t* test with appropriate Bonferroni corrections. For all the above measures, statistical significance was set at $p < 0.05$. SPSS 17 for Windows 7 (SPSS Inc., Chicago, USA) was used to conduct the statistical analysis. Data are presented in the text and figures as means and standard errors.

Results

EMG patterns

Figure 2 shows EMG patterns for the tibialis anterior (TA) and biceps femoris (BF) muscles recorded during all the experimental conditions. Anticipatory activation of TA and BF was seen in the full vision (FV) and high-frequency strobe light (HFS) conditions. At the same time, activation of muscles was delayed in the low-frequency (LFS) strobe light and eyes open in dark (EOD) conditions.

Onset of muscular activity

The muscle onset times calculated for all the subjects are shown in Fig. 3. In the dynamic cue conditions (FV and HFS), almost all the muscles showed anticipatory activity. The earliest activity in the FV condition was seen as an inhibitory response in the ES muscle at 98 ± 47 ms before perturbation, whereas in HFS condition the earliest activity was noticed in the RF muscle at 89 ± 34 ms before T_0 .

In the static cue condition (LFS), the majority of the muscles showed activity only after T_0 with the exceptions of BF and RF, which were inhibited at (9 ± 21 ms) or activated at (15 ± 20 ms) respectively, before the perturbation.

In the condition where no external visual cues were available (EOD), all the muscles showed activity only after the perturbation onset with the ES muscle showing the most delayed activity at 98 ± 13 ms after T_0 .

PCA validity was confirmed by visual inspections of the scree plots. On an average, three principal components (PCs) (Table 1) accounted for 79 % of the total variance in the muscle activation space in the HFS condition and 77 % of the total variance in the FV condition.

The first PC in the HFS condition showed high loading values for ES, ST, RF, BF and GM, whereas in FV condition the first PC was significantly loaded by TA, EO, MG and RA

muscles. The second PC in HFS condition showed high loading values for the muscle onsets of RF, BF, EO, TA and MG, whereas in FV condition the second PC was loaded mainly by BF, ES and RA. The third PC was loaded significantly higher in HFS condition by BF, RA and GM muscles, but it was loaded by ST, RF and GM in FV condition.

It is important to note that a co-contraction pattern was seen especially in the second and third components. A co-contraction was defined as a pattern with significant loading coefficients on the same PC with the same sign (positive or negative) for two muscles with opposing actions at a particular joint (ankle, knee or hip) (Krishnan et al. 2012).

EMG integrals

Integrals of EMG for the four experimental conditions are shown in Fig. 4. EMG integrals were larger in the dynamic cues conditions (FV and HFS) than in the static cues (LFS) and no cues (EOD) conditions. A main effect of conditions (Table 2) was seen in GM ($F_{3,27} = 8.24$, $p < 0.0001$), TA ($F_{3,27} = 9.49$, $p < 0.0001$) and RF ($F_{3,27} = 6.45$, $p = 0.002$). Further analysis revealed that this effect was primarily due to significant differences between the dynamic cues (FV and HFS) and no cue (EOD) conditions. Thus, significantly larger EMG integrals in GM ($p = 0.01$ and $p = 0.04$) and TA ($p = 0.015$ and $p = 0.001$) were observed in the dynamic cue conditions (FV and HFS, respectively) when compared to the no cue condition (EOD).

There were notable significant differences in the EMG integrals between the various epochs (Table 2). Overall, when epochs were compared, APA2 epoch showed larger muscle activity than APA1 epoch. Significantly ($p < 0.05$) larger EMG activity in APA2 epoch was recorded for EO, ES, GM, RA, RF and TA. There were statistically significant ($p < 0.05$) interactions between epochs and conditions for TA, RF, BF, GM, RA and EO.

Center of pressure displacements

Figure 5 shows changes in the position of the CoP in all experimental conditions. Early backward CoP displacements could be seen in FV and HFS conditions. The CoP displacement at the moment of perturbation (CoP T_0), reflecting anticipatory changes in the body position, revealed a significant main effect of cue conditions on APAs ($F_{3,27} = 14.29$, $p < 0.0001$). The displacement at T_0 was the smallest (0.003 ± 0.001 m) in the no cue condition (EOD), being significantly smaller than the CoP displacement observed in the dynamic cue conditions, FV (0.014 ± 0.002 m, $p = 0.006$) and HFS (0.018 ± 0.002 m, $p = 0.001$). Although the anticipatory CoP displacement in the static cue condition (LFS) was smaller (0.008 ± 0.002 m) in comparison with the dynamic cue conditions, the difference was not statistically significant.

The magnitudes of the CoP peak for FV, HFS, LFS and EOD were 0.04 ± 0.003 m, 0.04 ± 0.003 m, 0.05 ± 0.004 m and 0.06 ± 0.003 m, respectively. The peak of the CoP change recorded after perturbation (that is compensatory) showed a significant main effect of various cue conditions ($F_{3,27} = 40.04$, $p < 0.0001$). Further pair-wise comparison revealed that when the subjects were provided with dynamic cues (FV and HFS), the CoP peaks were significantly smaller when compared with static cues ($p = 0.014$ & $p = 0.003$, respectively) and no cues (EOD) ($p < 0.0001$ for both). In addition, the CoP peak for the no cue condition showed significantly larger displacement than static cue condition ($p = 0.011$).

Discussion

The results of the experiment reinforce previous findings on the importance of vision in control of vertical posture and provide evidence that feed-forward postural control in standing is modified due to the presence of different visual cues. In particular, the outcome

of the study revealed that the availability of the dynamic visual cues was associated with considerable anticipatory activation of muscles producing large anticipatory CoP displacements. However, when static visual cues were provided, the anticipatory activation of muscles and CoP displacements were reduced significantly. Finally, when no visual cues were available, there was a complete absence of APAs. Thus, our hypothesis that the ability to generate anticipatory postural adjustments is reduced in conditions with static as compared to dynamic visual cues was supported.

Role of vision in counteracting external perturbations

The role of vision in providing the CNS with continuously updated information regarding the position and movements of the body's segments and its relationship with the environment while maintaining balance is well documented. Thus, when people stand with their eyes closed, the postural sway increases by 20–70 % as compared to standing with eyes open (Paulus et al. 1984; Magnusson et al. 1990; Lord et al. 1991). Moreover, it was demonstrated that modifying visual information by moving visual field induces a powerful sense of self motion resulting in significant increases in body sway (Wei et al. 2010). In addition, previous research provides a plethora of evidence about the importance of visual information in restoring vertical posture after external perturbation is applied to the body (Clement et al. 1985; Bardy et al. 1999; Schmid et al. 2007).

At the same time, the literature on the role of vision in generation of APAs is limited. This is partially due to the fact that the vast majority of previous APA studies were based on utilizing self-initiated movements to induce body perturbations (Aruin and Latash 1995; Strang and Berg 2007; Klous et al. 2011). However, visual information is not required to generate APAs in response to self-initiated movements of the body segments, for example arm movements. Therefore, to a large extent, studies involving self-induced perturbations cannot provide information on the role of vision in the generation of APAs.

On the contrary, using a method involving external body perturbations allows the assessment of the role of vision in the generation of APAs and subsequently CPAs (Compensatory Postural Adjustments). Thus, it was shown in experiments involving catching a load, that APAs were absent when vision was not available. However, when visual information about the moment of the load release was provided, the subjects were able to generate APAs (Aruin et al. 2001). Moreover, it was recently shown that when vision was available, strong APAs were present which implied that the CNS was aware of the forthcoming body perturbation and had already activated the postural muscles for any adverse effects and the generated CPAs were smaller in magnitude. However, when visual information about the onset of the external perturbation was not known to the subjects (they were standing with eyes closed), the CNS failed to generate APAs and thus the CPAs were massive in magnitude (Santos et al. 2010a, b).

The outcome of the current experiment with full vision also demonstrates the importance of vision in the generation of APAs in relation to the predicted external perturbation. Thus, when the subjects were able to see the pendulum, they showed strong APAs evidenced by large anticipatory activation of muscles and substantial CoP displacements before the onset of the external perturbation. The generation of strong APAs resulted in more efficient maintenance of vertical posture confirmed by smaller magnitudes of CoP displacement after the perturbation.

Role of quality of visual information in generation of APAs

The current study demonstrated that not only availability of visual information *per se* affects generation of APAs in the case of external body perturbations, but also the quality of the

available visual information is an important element in maintenance of vertical posture. In particular, the outcome of the study revealed that certain visual cues allow an individual to utilize strong anticipatory postural adjustments needed for efficient control of vertical posture. Thus, when visual cues were dynamic (full vision, FV and high-frequency strobe light condition, HFS), APAs were generated. Quite the opposite, when static cues were provided (low-frequency strobe light condition, LFS), APAs were significantly diminished.

The differences in the APA generation could be explained by the alterations in the quality of visual information about the pendulum release. Thus, the results of the PC analysis suggest that different visual cues are associated with different loading responses in the studied muscles which could explain that the cues were qualitatively different. For example, in FV, the PC1 was significantly loaded for lower leg and trunk muscles, while in the HFS, it was loaded with trunk and thigh muscles (Table 1). PCA also demonstrates that there were differences in the co-contraction of muscles between the conditions: In FV, it was observed in the muscles around the ankle joint, whereas in HFS, it was around the knee joint. Based on this, it is possible to suggest that depending on the type of visual cues available, the CNS minimizes the negative consequences of a predicted postural perturbation by prioritizing the activation of different muscle groups. Thus, when the pendulum was fully visible in the FV condition, anticipatory activation of muscles around the ankle joint played a major role, whereas when high-frequency stroboscope flashes were available, larger muscle groups around the knee joint were activated.

Temporal parameters of visual cues are also crucial for the generation of APAs. Thus, when dynamic visual cues are available continuously either in a well-lit environment or when a strobe light is set at high frequency, precise information about the moment of the pendulum release becomes available, which results in the generation of strong APAs. In our study, dynamic visual cues were available in the full vision (FV) and high-frequency (66.67 Hz) strobe light (HFS) conditions allowing the subjects to see the pendulum either continuously (FV) or intermittently (HFS) during its entire movement until the pendulum hit the body. The existence of APAs in FV conditions is supported by the outcome of numerous previous experiments (Aruin and Latash 1995; Benvenuti et al. 1997; Toussaint et al. 1998; Yiou et al. 2009), while the current study demonstrated that dynamic cues allow the generation of decent APAs.

On the contrary, when the strobe light is set at the frequency less than 9 Hz (e.g., 5.83 Hz as it was in the current experiment), utilization of such static cues could produce errors in detecting movements of objects (Cian et al. 1997). As such, in the LFS condition, the particular moment of the pendulum release might not be known to the subjects, thus resulting in diminished ability to predict the consequences of the perturbation and generate strong APAs.

It is known that the CNS generates APAs by releasing a program that is time-locked to the expected body perturbation; such an ability to generate APAs is learned during childhood (Schmitz et al. 1999; Hadders-Algra 2005) and is used by healthy individuals throughout their life. In the current study, the subjects knew the moment of the perturbation in HFS which made it possible for them to estimate the time when the pendulum is going to contact with his/her body. As such, it is not surprising that obtaining precise information about the pendulum release resulted in healthy young subjects being able to generate strong APAs. In addition, previous experiments suggest that when the subjects could see the object during the first 10 cm of its trajectory (which was approximately 140 ms after the object was released by an experimenter), APAs timed appropriately with respect to the moment of load impact were generated (Aruin et al. 2001). Furthermore, it was reported that kinematics of the falling object is taken into account by the CNS to estimate the time before contact with

that object (Zago et al. 2004). Thus, the ability to see the pendulum path might help in obtaining information needed for generating APAs.

When visual cues about the moment of the pendulum release are provided by LFS, the time the subjects were able to see the moving pendulum after it was released was about 85 ms. It appears that this time was not enough to obtain precise information about the pendulum release and to trigger APAs. This conclusion is in line with the literature describing that the “time pressure” conditions (induced by the instructions to perform arm lifts under a simple reaction-time instruction) were associated with the inability of the subjects to generate the regular pattern of APAs (De Wolf et al. 1998).

There are some study limitations which should be taken into consideration. First, we performed experiments in a dark room. While walking in a poorly lit room is a common task for many activities of daily living, dealing with external perturbations in a completely dark room is not very common. As such, while the study outcome provides an insight into the use of visual information in the control of vertical posture, additional studies performed in a room with some light are needed. Second, while we were able to investigate the role of static and dynamic cues in control of posture, only two frequencies of the stroboscope light were used, suggesting a need to further investigate the effect of visual cues at different frequencies. Thus, there is a need for a future study focused on understanding of how different frequencies of static (<9 Hz) and dynamic (>9 Hz) visual cues affect APAs. Moreover, the stroboscope needs to be synchronized with the moment of the release of the pendulum so that the appearance of the light and dark phases of the flashes is better controlled. Third, since the stroboscope induced continuous change in the lighting conditions, it is not known how APAs are generated when only a single light of certain duration is provided.

Conclusion

In our experiment, we altered visual cues to investigate their role in control of vertical posture in humans. The outcome of the study revealed that when dynamic cues are available, it is easier for the CNS to predict the upcoming perturbation and generate APAs than when static cues are available. This conclusion is supported by the corresponding changes in the EMG activity and CoP displacements. The outcome of the study will help understand how different visual cues can affect generation of APAs and thus play a role in control of vertical posture.

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Fig. 1. Schematic diagram of the experimental setup. The subjects stood with their arms at their sides, and the pendulum impact was applied to their shoulders. Visual conditions were manipulated. l is the length and m is an additional mass (5 % of subject's body weight)

Fig. 2. EMG patterns (averaged across three trials for a representative subject) for the TA and BF muscles of the *right side* are presented across all the visual cues conditions. *Vertical line at T_0* indicates the moment of pendulum impact. EMGs are in arbitrary units (*y*-axis) and time is in ms (*x*-axis)

Fig. 3. Muscle latencies for the four experimental conditions. Note that for the EOD and LFS conditions, the onset of activity for all studied muscles is after the perturbation (T_0). The onsets of activity of the majority of studied muscles in the conditions with FV and HFS are before the perturbation (T_0)

Fig. 4. Mean normalized EMG integrals of RF, BF, TA and GM during the four visual conditions for all subjects. *Each column* represents the IEMG_{NORMS} for 150 ms of the APA1 and APA2 epochs with its standard *error bars*

Fig. 5.

a CoP traces for a representative subject are presented across all the visual cues conditions. *Vertical line* at T_0 indicates the moment of pendulum impact. **b** Mean CoP displacement at T_0 is shown as mean with standard errors. CoP negative values correspond to backward displacements. *Asterisk* indicates statistical significance at $p < 0.05$ in comparison with EOD condition

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Table 1

PC analysis for muscle onsets for the FV and HFS conditions

Muscles	Components (FV)			Components (HFS)		
	1	2	3	1	2	3
TA	0.938	0.314	0.166	-0.071	0.774	0.009
EO	0.857	-0.247	-0.168	0.282	0.793	0.162
MG	0.605	0.035	-0.010	-0.268	0.681	-0.347
BF	-0.135	0.887	-0.068	-0.583	0.547	0.457
ES	0.341	0.807	-0.082	0.884	0.076	0.272
RA	0.617	-0.630	0.040	-0.246	-0.017	0.945
ST	0.255	-0.058	0.928	0.891	-0.109	-0.093
RF	-0.389	0.386	0.754	0.622	0.573	-0.398
GM	-0.042	-0.289	0.620	0.460	-0.067	0.772

Loading factors are presented for the first three PCs. Loadings over 0.5 are shown in bold

Table 2

Repeated-measures ANOVA of IEMG_{NORMS} for conditions, epochs and their interactions

Muscles	Conditions		Epochs		Conditions × Epochs	
	$[F_{3,27}]$	p	$[F_{1,9}]$	p	$[F_{3,27}]$	p
TA	9.487*	<0.0001	11.935*	0.007	4.771*	0.009
MG	2.325	0.097	1.513	0.25	0.303	0.823
RF	6.454*	0.002	20.019*	0.002	7.805*	0.001
BF	0.596	0.623	0.54	0.481	4.296*	0.013
ST	0.417	0.742	2.155	0.176	0.134	0.939
GM	8.238*	<0.0001	17.702*	0.002	6.755*	0.002
RA	1.684	0.194	12.256*	0.007	5.724*	0.004
EO	1.733	0.184	17.786*	0.002	5.576*	0.004
ES	1.053	0.385	9.034*	0.015	1.089	0.37

The results are shown for the four experimental conditions: FV, EOD, LFS and HFS and for the two epochs: AP1 and APA2