Research Article

Human Vestibulo-Ocular Reflex Adaptation: Consolidation Time Between Repeated Training Blocks Improves Retention

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ABSTRACT

We sought to determine if separating vestibulo-ocular reflex (VOR) adaptation training into training blocks with a consolidation (rest) period in between repetitions would result in improved VOR adaptation and retention. Consolidation of motor learning refers to the brain benefitting from a rest period after prior exposure to motor training. The role of consolidation on VOR adaptation is unknown, though clinicians often recommend rest periods as a part of vestibular rehabilitation. The VOR is the main gaze stabilising system during rapid head movements. The VOR is highly plastic and its gain (eye/head velocity) can be increased via training that induces an incrementally increasing retinal image slip error signal to drive VOR adaptation. The unilateral incremental adaptation technique typically consists of one 15-min training block leading to an increase in VOR gain of ~10 % towards the training side. We tested nine normal subjects, each over six separate sessions/days. Three training protocols/sessions were 5 min each (1 × 5-min training) and three training protocols/sessions were 55 min each. Each 55-min protocol comprised 5-min training, 20-min rest, 5-min training, 20-min rest,

5-min training (3 × 5-min training). Active and passive VOR gains were measured before and after training. For training with consolidation breaks, VOR gain retention was measured over 1 h. The VOR gain increase after 1 × 5-min training was 3.1 ± 2.1 % ($P < 0.01$). One might expect that repeating this training three times would result in ×3 total increase of 9.3 %; however, the gain increase after 3 × 5-min training was only 7.1 ± 2.8 % ($P < 0.001$), suggesting that consolidation did not improve VOR adaptation for our protocols. However, retention was improved by the addition of consolidation breaks, i.e. gains did not decrease over 1 h ($P = 0.43$). These data suggest that for optimal retention VOR adaptation exercises should be performed over shorter repeated blocks.

Keywords: vestibulo-ocular reflex (VOR), VOR adaptation, VOR training repetition, VOR training consolidation, optimal VOR adaptation training parameters

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INTRODUCTION

The vestibulo-ocular reflex (VOR) maintains images stable on the retina during head movement by rotating the eyes in the opposite direction to the head. The VOR response can be trained (i.e. adapted)

up or down using a visual-vestibular mismatch stimulus, which has typically been induced by the use of magnifying, minifying or reversing lenses (Gauthier and Robinson 1975; Gonshor and Melvill Jones 1976a, b; Paige and Sargent 1991). Recent studies have induced visual-vestibular mismatch to drive a gradual increase in the VOR gain (eye/head velocity) by coupling the movement of a visual laser target with head motion (Schubert et al. 2008a; Migliaccio and Schubert 2013, 2014; Fadaee and Migliaccio 2016; Mahfuz et al. 2017, 2018). The visual laser target velocity, initially equal in magnitude but opposite in direction to head velocity, increases by 10 % every 90 s for a total training time of 15 min. These studies have mostly employed active (self-generated) transient head impulses (Halmagyi and Curthoys 1988) as the vestibular training stimulus because these have the same frequency and velocity content of head motion encountered in daily life (Grossman et al. 1988). This method, known as the incremental VOR adaptation technique, drives the normal VOR gain to increase significantly towards the side being trained/adapted (i.e. either left, right or both) by ~10 %.

VOR adaptation exercises are strongly recommended as part of vestibular rehabilitation for patients with peripheral vestibular organ/nerve hypofunction (Hillier and McDonnell 2011, 2016; McDonnell and Hillier 2015). The effect of current gaze stability exercises on improving active VOR gain is limited (Schubert et al. 2008b); however, existing data suggest using active head rotation and gaze stabilising exercises improve postural control (Matsugi et al. 2017) and reduce fall risk (Herdman et al. 2003, 2007; Hall et al. 2010). In addition to gaze stability exercises, patients with vestibular symptoms are encouraged to perform daily activities that require substantial head movement, e.g. a brisk walk. Current clinical practice guidelines specify clinicians prescribe a home exercise program of gaze stability exercises for a minimum of three times per day for a total of 12 min per day in patients with acute/subacute vestibular hypofunction, whereas for patients with chronic vestibular hypofunction, the recommendations are a minimum of 20 min per day (Hall et al. 2016). No study has examined whether the 12 to 20-min exercises should occur in a single large block or should be split into smaller time blocks and repeated with a brief time interval to allow for consolidation.

The goal of this study was to determine if separating VOR adaptation training over three repeated 5-min blocks with 20-min rest in between to allow a 'consolidation effect' would improve VOR adaptation and retention. We measured the active (predictable) and passive (unpredictable, externally imposed head impulse) VOR before and after unilateral incremental VOR adaptation training. We also

measured short-term retention of the active and passive VOR gain increases over 1 h immediately after adaptation training.

METHODS

Subjects

Nine normal subjects (mean age 33 years, range 24–44 years) were recruited to participate in this study. Each subject participated in six separate sessions, separated by at least 3 days with sessions not repeated. These subjects did not have any history or clinical signs of vestibular abnormality. None of the subjects were taking medication that could have affected vestibular adaptation mechanisms. Participation in this study was voluntary and subjects gave written informed consent before participating as approved by the University of New South Wales Human Ethics Committee.

Recording System

Head and eye rotations were measured using the EyeSeeCam system (Denmark), with the camera placed over the left eye (Bartl et al. 2009). The EyeSeeCam system consisted of a 220 Hz digital video camera, infra-red LEDs to illuminate the eye, an infra-red mirror to reflect the eye image to the camera and an inertial measurement unit to measure 3D (yaw, pitch and roll) angular head velocity. All components were rigidly mounted onto a lightweight swim goggle frame and silicon putty (Surgipack, Australia) was placed between the frame and face to minimise slip and add some comfort to the tight fit, especially since subjects wore the goggles for the duration of each session lasting up to two and a half hours. Horizontal and vertical eye positions were calibrated by having subjects fixate (goggle-mounted laser projected) visual targets at known angles with respect to the subject. The calibrated eye and head data were digitally filtered with a 50-tap zero-phase low pass FIR filter with a bandwidth of 50 Hz.

Training System

A digital portable laser target device controlled the position of a laser target directed onto a matte-white projection screen (2.4×2.4 m) 1 m in front of the subject (Analog version: Migliaccio and Schubert 2014; Digital version: Mahfuz et al. 2017, 2018). The device consists of a head unit (strapped securely to the forehead) and a base (or control) unit. The head unit consists of a laser mounted in a fixed position relative to, and aimed at the centre of, an electrostatic MEMS micro mirror (Mirrorcle Technologies Inc.,

USA), and a 9D IMU (3D accelerometer, 3D gyroscope and 3D magnetometer Inertial Measurement Unit; STMicroelectronics, USA). Information from the IMU is processed so that 3D head orientation with respect to space can be calculated at 250 Hz to within 0.1° . The head orientation is used to drive the mirror and hence laser target position with respect to the head. The base unit provides auditory feedback when head impulse peak-velocity is below $120^\circ/\text{s}$ or above $180^\circ/\text{s}$.

Active and Passive VOR Adaptation Training Protocols

Each subject underwent six test sessions on separate days in pseudo-randomised order. Each test session implemented a variation of the unilateral incremental VOR adaptation training technique as previously described (Migliaccio and Schubert 2013, 2014; Fadaee and Migliaccio 2016). In brief, using the head impulse test (Halmagyi and Curthoys 1988), the active and passive VOR gain was measured before and after active VOR adaptation training. Passive VOR gain testing prior to (and after) training required head impulses delivered manually in the horizontal canal plane, i.e. leftward and rightward. Subjects were trained to perform active head impulses similar in profile to the passive head impulses (per Fig. 1). During VOR testing, a visual fixation target (laser target) located straight ahead and at eye level was provided. This target disappeared when the head rotated 0.6° away from neutral.

Unilateral VOR adaptation training consisted of a series of alternating leftward and rightward active head impulses starting from a neutral position, i.e. only outward impulses were applied. The adapting side was pseudo-randomised, leftward or rightward, across subjects (e.g. rightwards for 5/9 subjects). For each head impulse, subjects were instructed to maintain visual fixation of the laser target whose horizontal position was a function of horizontal head position, head impulse direction and adaptation gain (eye/head angular speed) demand. For rotations towards the non-adapting side, the gain demand was fixed to unity (i.e. driving no adaptation), whereas for rotations towards the adapting side, it incrementally increased starting from unity at epoch one. For training protocols 1 to 3, the total adaptation training time was 5 min. For protocol 1, the training consisted of 10 epochs each lasting 30 s. For each epoch the gain demand increased by 0.1, so that by epoch 10 it was 1.8. For protocol 2, training consisted of 5 epochs each lasting 60 s, with the gain increasing by 0.2 per epoch (epoch 10 gain demand = 1.8). For protocol 3, training also consisted of 5 epochs each lasting 60 s, but with the gain increasing by 0.1 per epoch (epoch

10 gain demand = 1.4). For training protocols 4 to 6, the adaptation exercises lasted 15 min, but with consolidation periods the total adaptation training time was 55 min. Protocol 4 consisted of repeating three times protocol 1, with 20 min in between repetitions. Similarly, protocols 5 and 6 consisted of repeating three times protocols 2 and 3, respectively, with 20 min in between. Apart from the laser target all training (including the consolidation period) and testing was performed in complete darkness. (See Table 1 for description of the six sessions/protocols).

Post-adaptation Training VOR Retention Test Protocols

For protocols 4 to 6, the active and passive VOR was measured immediately after training and then at a regular 20-min time interval. A previous human study showed that when the VOR gain was tested every 20 min, starting immediately after the completion of adaptation training, the VOR gain significantly decreased after 40–60 min (Mahfuz et al. 2018). We measured the active and passive VOR gain at 0, 20, 40 and 60 min after adaptation training. A stop watch was used with pre-set auditory alarms to ensure VOR testing started on time. Subjects were kept in complete darkness between testing while still wearing the video-oculography system and training device that controlled the laser target during testing. Subjects were kept alert throughout this 1-h period by listening to an engaging podcast (i.e. not music) of their choice, while the experimenter spoke and regularly asked them questions to ensure their alertness.

Data Analysis

Horizontal angular eye position was differentiated and the onset of each head impulse was calculated by fitting horizontal angular head velocity magnitude to a polynomial curve versus time. The point where the magnitude of the fitted curve was greater than 2 % of the curve's peak magnitude (typically this threshold was $4^\circ/\text{s}$) was defined as the impulse onset (Aw et al. 2003; Migliaccio et al. 2003). Only head impulses with peak magnitude between $150^\circ/\text{s}$ to $300^\circ/\text{s}$ were included in the analysis. Traces with saccades occurring inside a window starting at 100 ms before impulse onset and ending at impulse peak magnitude (typically 100 ms after onset) were also removed. Head velocity traces that did not fit the velocity criteria and eye traces containing blinks and other artefacts, together affecting ~20 % of the data, were removed, along with their corresponding eye and head traces. The instantaneous VOR gain was calculated as the magnitude of eye velocity divided by head velocity. The impulse VOR gain was calculated as the median of the

FIG. 1. Passive (first and third rows) and active (second and fourth rows) VOR responses immediately before (left column), and immediately after (right column) VOR training using protocols 1 (top two rows) and four (bottom two rows) in one subject. The 5-min training blocks for protocols 1 and 4 are identical; however, for protocol 4,

the training block was repeated three times with 20 min between repetitions. The passive VOR gain increase after protocol 4 was 9.3 % compared to 3.4 % for protocol 1, representing a 2.7 increase. The active VOR gain increase after protocol 4 was 8.6 % compared to 4.4 % for protocol 1, representing a 2.0 increase

instantaneous VOR gains calculated during the 30-ms period (at 220 Hz, this corresponds to 6 to 7 instantaneous gain values) immediately prior to impulse peak magnitude. The percentage of VOR gain change for each side (adapting or non-adapting) was calculated by dividing the post-training by the pre-training VOR gain, subtracting by 1, and multiplying by 100. A positive

percentage indicated an increase in VOR gain due to adaptation training.

Statistical Analysis

Statistical analysis was performed using SPSS version 23 (IBM, USA) and Excel 2013 (Microsoft, USA)

TABLE 1

The six protocols shown were presented in pseudo-randomised order. Protocols 1–3 consisted of a single block of 5-min active head impulse training, whereas protocols 4–6 consisted of three repeated 5-min blocks of training with 20-min consolidation time between repetitions. N/A means that a value for that cell is not applicable

Prot.	Epochs	Epoch duration (s)	Epoch increase	Repetitions	Time between repetitions	Total training time (min)
1	10	30	0.1	N/A	N/A	5
2	5	60	0.2	N/A	N/A	5
3	5	60	0.1	N/A	N/A	5
4	10	30	0.1	3	20 min	55
5	5	60	0.2	3	20 min	55
6	5	60	0.1	3	20 min	55

software. Normal Q-Q plots of both the VOR gain and percentage gain change showed normal distributions. A linear mixed model (LMM) with repeated measures was used to analyse the VOR gain data. Independent variables included the following: subject ID, VOR training *protocol* ('1', '2', '3', '4', '5', '6'), VOR *testing* type ('active', 'passive'), head rotation *side* ('adapting', 'non-adapting') and *time* ('pre-training', 'post-training'). To analyse VOR retention, the *time* variable was modified ('pre-training', '0', '20', '40', '60'). The dependent variable was either gain or percentage gain change. All variables were included in the LMM initially and those found insignificant were subsequently removed. Only the interaction effects found to be significant are included in the results. Paired *t* tests were performed on the pre- and post-training VOR gains and the percentage increases for each protocol using least significant difference (LSD) to correct for multiple comparisons. Pooled data are described as mean $\pm$ 1 SD.

RESULTS

Pre-adaptation Training VOR

There were no differences in VOR gains between leftward and rightward (ANOVA: $F_{1,188} = 0.01$, $P = 0.9$) and between active and passive (ANOVA: $F_{1,188} = 0.03$, $P = 0.87$) head impulses. However, there were between-subject differences in pre-adaptation gains (ANOVA: $F_{8,188} = 15.2$, $P < 0.001$), with means ($\pm$ SD) ranging from 0.89 ± 0.03 to 0.96 ± 0.03 . The mean pre-adaptation VOR gain pooled across subjects was 0.95 ± 0.06 . Power analysis indicates that with 9 subjects, an 8.3 % increase in VOR gain would be detected with 80 % power ($\mu_1 = 0.95$, $\mu_2 = 1.029$, $SD = 0.06$, $\alpha = 0.05$, two-sided test). However, after normalising gains (scaling by a fixed number for each subject) so that the mean pre-adaptation gain pooled across all conditions was equal to unity for each subject, SD across subjects reduced to 0.03 and a 3.9 % increase in

VOR gain could be detected with 80 % power ($\mu_1 = 1.0$, $\mu_2 = 1.039$, $SD = 0.03$, $\alpha = 0.05$, two-sided test).

Active and Passive VOR Training Retention in a Typical Subject

Figure 1 shows the active and passive VOR responses immediately before (left column) and immediately after (right column) VOR training using protocols 1 (top two rows) and 4 (bottom two rows) in a typical subject. The 5-min training blocks for protocols 1 and 4 are identical; however, for protocol 4, the training block was repeated three times with 20-min rest periods between block repetitions. The passive VOR gain increase after protocol 4 was 9.3 % (*t* test between pre-training and post-training gains, $P < 0.001$). This increase was 2.7 times larger than the 3.4 % increase (*t* test, $P < 0.005$) for protocol 1. There was no difference between active and passive VOR gain increases in this subject (*t* test, $P = 0.52$).

Active and Passive VOR Gain Adaptation for Each Training Protocol Across Subjects

Figure 2 shows VOR gain data from protocols 1 (top left panels), 2 (middle left panels), 3 (bottom, left panels), 4 (top right panels), 5 (middle right panels) and 6 (bottom right panels) across subjects. For each protocol (i.e. graph pair), the active (left graph) and passive (right graph) VOR gain pre- (white boxplot) and post-training (grey boxplot) are shown for head impulses towards the adapting (left side of graph) and non-adapting (right side of graph) sides. Significant increases between pre-training and post-training gains, as per multiple *t* test comparisons, are denoted by an asterisk. A linear mixed model analysis of the data showed *time* ('pre' vs 'post' training; $F_{1,103} = 19.9$, $P < 0.0001$), *side* ('adapting' vs 'non-adapting'; $F_{1,103} = 3.9$, $P = 0.0498$) and the interaction between the two (LMM: $F_{1,103} = 4.0$, $P = 0.0476$) significantly affected the VOR gain, suggesting that the gain change on the adapting

FIG. 2. VOR gain data from protocols 1 (top left panels), 2 (middle left panels), 3 (bottom, left panels), 4 (top right panels), 5 (middle right panels) and 6 (bottom right panels). For each protocol (i.e. graph pair), the active (left graph) and passive (right graph) VOR gain pre- (white boxplot) and post-training (grey boxplot) are shown for head impulses towards the adapting (left side of graph) and non-

adapting (right side of graph) sides across subjects. The boxplots show the median with 2nd and 3rd quartiles and whiskers showing the minimum and maximum gains, and below each boxplot pair the mean and SD percentage gain change is reported. * denotes a significant increase between pre-training and post-training gains

side changed due to training. The factor *protocol* (1–6; $F_{5,133} = 2.4$, $P < 0.05$) was also significant suggesting that the VOR gain increase depended on the protocol. There was no difference between the active and passive VOR gains (LMM: $F_{1,103} = 0.2$, $P = 0.68$).

Due to the variability of pre-adaptation gains across subjects, data were normalised for each subject/session by calculating the percentage VOR gain increase for each side (adapting, non-adapting). Using the normalised data, the factors *protocol* (LMM: $F_{5,59} = 7.7$, $P < 0.001$) and *side* (LMM: $F_{1,49} = 20.5$, $P < 0.001$) became highly significant. The difference between the active and passive VOR gains (LMM: $F_{1,49} = 1.3$, $P = 0.25$) remained insignificant.

When only analysing protocols 1–3, *side* remained significant (LMM: $F_{1,35} = 7.8$, $P < 0.01$), suggesting that

5 min of training significantly increases the VOR gain. However, *protocol* was not significant (LMM: $F_{2,39} = 0.9$, $P = 0.41$), suggesting these three protocols had the same effect on VOR gain increase. The average VOR gain increase across protocols 1–3 towards the adapting and non-adapting sides were 3.1 ± 2.2 and 1.0 ± 2.1 %, respectively. When only analysing protocols 4–6, *side* became highly significant (LMM: $F_{1,26} = 12.8$, $P < 0.001$) and *protocol* was not significant (LMM: $F_{2,43} = 0.5$, $P = 0.61$), suggesting that these three protocols had the same effect on VOR gain increase. The average VOR gain increase across protocols 4–6 towards the adapting and non-adapting sides were 7.1 ± 2.8 and 3.2 ± 3.0 %, respectively. The average percentage gain increase for protocols 4–6 was 2.2 ± 1.6 times larger than for protocols 1–3.

Retention of VOR Training Across Subjects

Figure 3 shows the normalised active (top) and passive (bottom) VOR gain percentage increases towards the adapting side after protocols 4–6 across subjects. VOR gains were measured every 20 min after adaptation training. The main factors that affected the VOR gain increase were *side* (LMM: $F_{1,100} = 22.7$, $P < 0.001$) and *protocol* (LMM: $F_{2,156} = 3.7$, $P < 0.05$), suggesting that the VOR gain increase was largest towards the adapting side and that the magnitude of that increase over 60 min depended on the protocol. Table 2 shows the mean and SD active and passive VOR gain percentage increases towards the adapting side for protocols 4–6 at each time point. Removal of protocol 5, resulted in *protocol* no longer being significant (LMM: $F_{1,96} = 0.1$, $P = 0.81$). For protocols 4–6, the factor *time* was not significant (LMM: $F_{3,100} = 0.9$, $P = 0.43$), suggesting that the VOR gain increase did not change with time, i.e. the gain increase was retained over 60 min. The gain increases pooled across time for protocols 4–6 were 6.7 ± 3.9 , 6.2 ± 3.0 and 6.9 ± 3.1 %, respectively.

DISCUSSION

In this study, three different 5-min unilateral incremental adaptation protocols (1–3) were used to increase the VOR gain. The VOR gain increase towards the adapting side was the same across these protocols at ~ 3 %. The same 5-min protocols above were repeated three times with 20 min between repetitions so that the adaptation training exercises took 15 min out of a total training time of 55 min, i.e. protocols 4–6. The VOR gain increase towards the adapting side was the same across these protocols at ~ 7 %, which was retained over 60 min. The percentage gain increase pooled across 60 min was lower for protocol 5, compared to protocols 4 and 6.

Adaptation Training

The different 5-min training sessions all resulted in a significant, albeit small ~ 3 % increase in VOR gain as detected by LMM. However, simple *t* tests applied to each 5-min protocol were unable to detect significant increases. There was also no detectable difference

FIG. 3. Normalised active (top) and passive (bottom) VOR gain percentage increases towards the adapting side immediately after completing training protocols 4 (white boxplot), 5 (light grey) and 6 (dark grey) across subjects. VOR gains were measured every 20 min after adaptation training. The boxplots show the median with 2nd and 3rd quartiles and whiskers showing the minimum and maximum gain percentage increases

TABLE 2

The mean and SD of the active and passive VOR gain percentage increases towards the adapting side for protocols 4–6 were measured every 20 min after adaptation training over 1 h

Time post-training		0 min	20 min	40 min	60 min
Active VOR gain increase (%)	Protocol 4	8.4 ± 3.3	7.9 ± 4.9	6.1 ± 3.8	5.4 ± 3.5
	Protocol 5	8.2 ± 2.9	7.3 ± 3.0	6.5 ± 3.6	5.5 ± 4.2
	Protocol 6	6.9 ± 1.7	8.9 ± 2.1	6.7 ± 1.8	7.1 ± 4.2
Passive VOR gain increase (%)	Protocol 4	7.0 ± 4.0	8.1 ± 3.9	5.8 ± 4.3	5.2 ± 3.6
	Protocol 5	6.4 ± 2.5	5.5 ± 2.0	5.0 ± 2.3	5.4 ± 3.2
	Protocol 6	5.5 ± 2.0	6.5 ± 3.2	6.6 ± 2.9	7.0 ± 5.3

between the 5-min training protocols. This failure to detect differences was likely in part because the signal to noise ratio for each protocol was low, i.e. the noise was ~2 %. The fact that the 5-min protocols resulted in a barely detectable significant (i.e. with LMM only) increase in gain suggests 5 min is the minimum duration for effective VOR adaptation training. The 3 % increase was about one third of the typical 10 % increase observed in prior studies using the same techniques, but where the training occurred over a single 15-min period (Mahfuz et al. 2017, 2018). By introducing a rest period immediately after training that resulted in only a small gain increase, risks losing some of that adaptation via normal visual feedback that seeks to drive the VOR gain down towards unity. To avoid this issue, we kept our normal subjects in complete darkness throughout the rest periods, but some loss can still occur. In patients with vestibular hypofunction, the situation is different because their starting gains are well below normal. After adaptation training, their gains would be closer to normal, albeit probably still below. Therefore, unlike normal subjects, patients exposed to a normal visual environment in between training blocks would not be expected to lose their increased gain. Rather, normal visual exposure should reinforce their training and perhaps drive their gains closer to normal (Mahfuz et al. 2018). The addition of 20-min consolidation periods between three 5-min training blocks resulted in a significant increase of ~7 % in VOR gain, which was ~30 % lower than that seen in prior 15 min training studies with ~10 % increase, suggesting that consolidation did not lead to increased VOR adaptation. In fact, the average percentage gain increase for protocols 4–6 was only 2.2 times larger than for protocols 1–3. At minimum, one might have expected a three times larger increase given that the 5-min adaptation exercises were repeated three times for protocols 4–6. The rest period in between exercises seems to have reduced VOR gain adaptation. A possible explanation is that each 5-min training block consisted of incremental gain adaptation training with starting gain demand equal to unity. In other words, the initial training period for blocks 2 and 3 drove a VOR gain

demand that was lower than at the end of block 1, in effect briefly driving adaptation in the opposite direction, i.e. down instead of up. We chose this approach because we thought it best represented how most vestibular patients would be asked to train at home. An alternate experimental design would have been to simply divide the typical 15-min training period into three blocks, so that each subsequent block starting gain demand was 10 % higher than the prior block ending gain demand. The disadvantage with that approach is that the starting gain demand would be further away from the subject's actual gain at the beginning of each training block (especially during the last block), resulting in gain demands too large for optimal adaptation. We did not measure the actual gain between training blocks because VOR testing drives gain down adaptation in normal subjects (Mahfuz et al. 2018). We hypothesise that the optimal approach would be to continuously measure the subject's active VOR gain during training and set the VOR gain demand to be 0.1 or 10 % greater. In this way, subjects would be able to recommence training starting at their current level of adaptation. Unfortunately, control of VOR gain demand based on instantaneous VOR response feedback was not possible with our training device.

Retention of Adaptation Training

In contrast to a prior study that examined retention using the same techniques (Mahfuz et al. 2018) and reported a significant decrease of ~4 % after 1 h, the loss of short-term (1 h) retention for protocols 4–6 was only ~1 % and not significant, suggesting that consolidation does improve retention. Although retention was evident for all three protocols tested, the percentage gain increase pooled across 60 min was lower for protocol 5, compared to protocols 4 and 6. The main difference between protocol 5 and protocols 4/6, was that the incremental gain demand increase per epoch was double, i.e. it was 0.2 rather than 0.1. This finding suggests that the magnitude of the incremental increase in gain demand affects VOR adaptation more so than the difference in epoch

duration (protocol 4 had half the epoch duration than protocols 5/6, i.e. 30 vs 60 s) and final gain demand (protocol 6 had half the final gain demand of protocols 4/5, i.e. 1.4 vs 1.9 and 1.8).

Implications for Vestibular Rehabilitation

Although the present study only tested subjects with normal VOR function, the findings reveal aspects of VOR adaptation and retention that have implications for VOR rehabilitation in patients with peripheral vestibular hypofunction. What is clear from this study is that using a small incremental increase of VOR gain demand during training is important to optimise VOR motor learning. We believe that most gaze stability exercise prescription asks patients to do exercises that over-challenge their VOR gain. For example, when a patient with a gain of 0.5 is asked to quickly move their head while viewing a stationary target, the gain demand is unity, i.e. double their actual gain. A large difference between actual gain and gain demand appears to hinder VOR adaptation, which might explain why chronic patients with, albeit incomplete vestibular lesions, rarely experience gain recovery. Our data suggests that challenging the VOR to increase in small increments of 0.1 (or 10 % of the subject's baseline gain) and starting at the subject's actual gain level results in better adaptation. However, with this type of training, it is important to note that exercises that work well over a single training block do not necessarily work well by simple repetition. Short-term changes/improvements in VOR adaptation between training blocks should be taken into account; otherwise, repeat exercises may be undoing some of the gain increase. If the exercises are tailored for repetition, then repeat training with a short rest period in between to allow for consolidation will likely result in optimal VOR adaptation and retention.

Conclusions

The main finding from this study is that consolidation between adaptation training blocks leads to improved retention. The retained gains are higher when the VOR gain demand increment during adaptation training is small. Our data support that reducing the error signal exposure time into three repeated 5-min blocks offered no improved motor learning compared to a single 15-min block. Taken together, these findings suggest that repeat training with a short rest time in between is beneficial, but exercises need to be specially tailored for this type of training.

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COMPLIANCE WITH ETHICAL STANDARDS

Participation in this study was voluntary and subjects gave written informed consent before participating as approved by the University of New South Wales Human Ethics Committee.

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