Research Article

Surface Electrical Stimulation Perturbation Context Determines the Presence of Error Reduction in Swallowing Hyolaryngeal Kinematics

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Purpose: Error-based learning (EBL) involves gradually reducing movement errors caused by a perturbation. When the perturbation has been unexpectedly removed, exaggerated movements occur in the opposite direction of a perturbation effect, known as aftereffects. Our goal was to determine whether the perturbation type impacts error reduction or aftereffects in swallowing hyolaryngeal kinematics.

Method: We perturbed peak hyolaryngeal elevation during swallowing in 16 healthy adults with surface electrical stimulation (SES) in 2 different ways during videofluoroscopy: intermittent SES (I-SES) was applied only during swallowing, and continuous SES (C-SES) was applied during swallowing

and during interswallow intervals. In C-SES and I-SES, the onset and offset of the perturbation were unmasked.

Results: Only the C-SES perturbation caused error reduction (gradually increasing peak elevation). Aftereffects were absent in both perturbations, unlike findings from our previous study with masked perturbation. Furthermore, the duration of laryngeal vestibule closure (dLVC) increased during the I-SES perturbation but was unchanged during C-SES perturbation.

Conclusion: EBL of swallowing airway protection events was strongly influenced by the context of the perturbation. These findings also elucidate how the relationship among critical swallowing airway protection events (hyoid peak, laryngeal peak, and dLVC) can be modified during EBL.

Throughout a person's lifetime, his or her neuromuscular system makes accurate movements through a process called error-based learning (EBL), often referred to as motor adaptation or adaptive motor learning. EBL is one form of learning within the larger field of motor learning, which focuses broadly on improving movement. EBL is based on assumptions that the nervous system predicts the outcome of a movement before the movement is made to prevent errors (Shadmehr & Mussa-Ivaldi, 1994). Then, after the movement has been made, the predicted outcome is compared to the actual movement that occurred, via sensory feedback, to assess whether the movement goal was achieved. In the presence of a continuous perturbation, EBL should minimize the differences between planned movements and the movement outcomes to minimize errors over several attempts (Shadmehr & Krakauer, 2008; Shadmehr,

Smith, & Krakauer, 2010). It is also noteworthy that EBL is often implicit, meaning learning is incidentally occurring without awareness of what specifically has been learned (Seger, 1994). This is in contrast with skilled learning training, in which a movement goal is explicitly provided and targeted during training (Annett, 1971). The majority of what researchers know about EBL is based on goal-oriented movements involving arm, leg, and eye function (Galea, Vazquez, Pasricha, de Xivry, & Celnik, 2011; Jayaram, Galea, Bastian, & Celnik, 2011; Morton & Bastian, 2004, 2006; Torres-Oviedo & Bastian, 2011). In these experiments, the movement task is perturbed, and, consequently, the error-reduction process occurs across several repeated trials.

The underlying mechanism thought to be responsible for this form of prediction is feed-forward control, for which the cerebellum is thought to be a critical neural substrate (Morton & Bastian, 2007). Feed-forward control plays a role in how the brain communicates control commands to muscles before a movement has been made. Thus, in feed-forward control, the command to alter the next movement is not based on the outcome of that movement (which is not yet known). Instead, it is based on what was learned from the experience(s) of the previous movement(s). In classic

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experiments that test feed-forward control in EBL, the study design often involves three phases including preperturbation (baseline), perturbation, and postperturbation, wherein the same task is repeated several times in each phase. Participants are typically unaware that a transition in the phases will take place. Neither the pre- nor the postperturbation phase involves any disruption to the movement goal, but the perturbation phase includes a disruption to the movement goal throughout. In this design, EBL is tested during the perturbation phase and at the beginning of the postperturbation phase. During the perturbation phase, EBL is shown as movements that gradually overcome the effect of the perturbation. For example, if the goal is to quickly elevate the right hand to shoulder level, then placing a load on that hand during the perturbation phase would initially limit elevation. However, EBL should cause increasingly higher hand elevation across a number of trials. Then, when the perturbation is suddenly and unexpectedly removed, EBL is evidenced by after effects early in the postperturbation phase. Aftereffects are exaggerated movements in the opposite direction of the perturbation effect, exceeding preperturbation levels (Bastian, 2008). Using the previous example of hand elevation, EBL aftereffects would be shown if the hand overshoots the shoulder. This aftereffect demonstrates feed-forward control in EBL because the predictions and movement commands were based on experiences in the perturbation period in which excessive force was needed to elevate the loaded limb. Experiments such as these demonstrate how EBL is based on sensory predictions about movement expectations that are gradually aligned with movement outcomes (Flanagan & Wing, 1997; Krakauer, Ghilardi, & Ghez, 1999; Shadmehr & Mussa-Ivaldi, 1994; Wolpert, Ghahramani, & Jordan, 1995).

Some manipulations to the perturbation period have been made in EBL studies to understand how error reduction and aftereffects vary. In a multiple perturbation EBL paradigm, Schlerf, Galea, Bastian, and Celnik (2012) posited that the cerebellum is more responsive to a large, abrupt perturbation than to gradual or randomly presented perturbations. Rand, Shimansky, Stelmach, and Bloedel (2004) showed that predictable perturbations lead to error-reducing movements of all measured components of the wrist because feed-forward control was more accurate when predicting error reduction in subsequent trials. However, unpredictable perturbations did not provide a consistent learning experience for feed-forward planning, causing variable EBL outcomes (adaptation in only some wrist movement measures; Rand et al., 2004). Finally, awareness of the presence or absence of a perturbation influences the magnitude of aftereffects in visuomotor limb tasks (Criscimagna-Hemminger, Bastian, & Shadmehr, 2010; Kagerer, Contreras-Vidal, & Stelmach, 1997).

Understanding the role of perturbations on movement error reduction is inherently tied to improving movements in many domains, including skill learning, sports, and rehabilitation. In rehabilitation, therapists may determine that patients do not minimize errors over several attempts (i.e., falling, dropping objects) and may train patients to

predict potential errors before making the movements. Experiments in EBL help researchers to understand how intact sensorimotor systems reduce error and can be applied to rehabilitation training programs (Bastian, 2008). However, swallowing research has only recently examined the principles of motor learning for rehabilitation.

Normal swallowing involves hyolaryngeal elevation with precise timing to aid in airway protection (Kendall, McKenzie, Leonard, Goncalves, & Walker, 2000). The integration of sensory information (i.e., bolus properties) is critical for proper timing of airway protection during swallowing (Molfenter & Steele, 2011, 2012; Steele & Miller, 2010). In previous studies, we asserted that the motor plan for swallowing hyolaryngeal kinematics occurs before the bolus has entered the pharynx, possibly during the oral preparation and/or oral propulsion phases (Humbert, Lokhande, Christopherson, German, & Stone, 2012). EBL can help us to understand whether hyolaryngeal motor planning occurs even before the bolus has entered the oral cavity (i.e., experiences from previous swallows) and its impact on learning. Learning to plan to overcome a swallowing perturbation could be readily useful in dysphagia rehabilitation. This can be tested in an EBL paradigm that will specifically examine the role of feed-forward control in EBL for swallowing airway protection.

Previously, in healthy adults, we tested EBL by perturbing swallowing hyolaryngeal peak elevation using surface electrical stimulation (SES) on the neck across 20 consecutive perturbation trials (Humbert et al., 2013). Neck SES has been shown to perturb airway protection by restricting hyolaryngeal elevation during swallowing (Humbert et al., 2006). We found that continuous SES perturbation, applied during both swallowing and interswallow intervals, caused peak hyolaryngeal elevation that gradually increased toward preperturbation peak levels (Humbert et al., 2013). In this study, aftereffects were characterized by significantly higher peak hyolaryngeal elevation that exceeded preperturbation levels when the perturbation was unexpectedly removed. However, it is unknown whether other types of SES perturbation would cause different EBL outcomes on swallowing hyolaryngeal elevation. This has relevance to dysphagia rehabilitation because neck SES is used to treat dysphagia using various stimulation protocols with conflicting reports about improvements in swallowing ability (Clark, Lazarus, Arvedson, Schooling, & Frymark, 2009; Huckabee & Doeltgen, 2007; Humbert, Michou, MacRae, & Crujido, 2012; Poorjavad, Talebian Moghadam, Nakhostin Ansari, & Daemi, 2014; Tan, Liu, Li, Liu, & Chen, 2013).

The goal of this investigation was to manipulate EBL paradigms to examine the effects on swallowing hyolaryngeal kinematics in two important components of EBL: (1) gradual return to preperturbation levels (error reduction) during the perturbation phase and (2) aftereffects when the perturbation is unexpectedly removed. We tested gradual return to preperturbation levels under two conditions: continuous surface electrical stimulation (C-SES) perturbation, which is SES during both swallowing and interswallow intervals, and intermittent surface electrical stimulation

(I-SES) perturbation, which is SES only during swallowing but not during interswallow intervals. Aftereffects were examined by completely removing the perturbation without masking its removal with sensory cues as in our previous investigation (Humbert et al., 2013). We hypothesized the following: (1) C-SES perturbation would result in gradual return to preperturbation hyolaryngeal peak levels, but I-SES perturbation would not, and (2) unmasked perturbation removal would not result in aftereffects. Our rationale for both hypotheses is based on evidence that swallowing airway protection kinematics, and possibly feed-forward error-reduction planning, are modulated using sensory information that occurs before the onset of the swallow (Humbert, Lokhande, et al., 2012). Also, previously discussed studies in other motor systems suggest that the type of perturbation modulates the extent to which feed-forward control is applied during learning. We also measured laryngeal vestibule closure (LVC) because it is an important airway protective event to which hyolaryngeal elevation contributes. The outcomes from this study are significant because they could reveal whether specific forms of perturbations applied with SES, widely used for swallowing treatment, are more amenable to error reduction in swallowing airway protection than others. These outcomes also emphasize the importance of using objective, instrumental techniques to measure hyolaryngeal function. In this study, we used videofluoroscopy (video x-ray) because it is both clinically relevant and superior to other imaging methods for observing the progress and outcome of treatments such as SES on swallowing airway protection.

Method

Ethical Approval and Participants

This study included 16 healthy adults (mean age = 25 years, range = 22–38; 4 men, 12 women) with no history of neurological disease, speech or swallowing impairment, chronic medical condition, or contraindications to SES. All participants signed written informed consents to participate in the study, which was approved by the Johns Hopkins School of Medicine Institutional Review Board. This study included only healthy adults and not patients with swallowing impairments to prevent increased aspiration.

Study Design

Each session began with a baseline of 10 swallows (preperturbation period), followed by a block of 20 perturbed swallows (perturbation period), then one swallow where the perturbation was removed to determine the presence of aftereffects (postperturbation). (See the study design in Figure 1.) All swallows were water in 5-ml amounts, infused to the anterior oral cavity with a small plastic tube to elicit and standardize swallowing for all 31 swallows. Participants did not suck on the tube to obtain the bolus. All swallows were cued verbally by the investigator after the bolus was in the oral cavity for approximately 2–3 s. The interswallow intervals were approximately 10 s in duration.

Figure 1. Schematic of study designs for intermittent surface electrical stimulation (I-SES) and continuous surface electrical stimulation (C-SES) conditions. Gray shaded regions denote administration of the perturbation.

Procedure

Electrical stimulation. SES (Ministim; Life-Tech, City, State) was administered to the anterior neck on the skin overlying the infrahyoid muscles (omohyoid, sternohyoid, sternothyroid, and thyrohyoid) to depress the hyolarynx at a sensory-motor stimulation level (Humbert et al., 2006; Ludlow et al., 2007). Electromyography artifact recording from muscles under the chin was monitored for each swallow to confirm the presence of stimulation during the study. The sensory-motor intensity level was individually determined and obtained by gradually increasing the amplitude to the highest level that could be tolerated without pain, leading to hyolaryngeal depression seen with videofluoroscopic imaging during simulation at rest.

Videofluoroscopy. We used videofluoroscopy to image hyolaryngeal movement. Videofluoroscopy is a radiographic technique (video x-ray) that allows imaging and analysis of swallowing kinematics. We obtained full-resolution, continuous fluoroscopic digital images in real time (30 frames per second) in the lateral plane. The image intensifier was focused on the oral cavity, pharynx, larynx, and just below the upper esophageal sphincter. A time stamp was superimposed onto images as a unique identifier of each frame. The extent of hyolaryngeal kinematics and LVC is best viewed with videofluoroscopy, compared to fiber-optic endoscopic evaluation of swallowing, another common clinical imaging technique for swallowing.

Conditions

Participants were randomly assigned to one of two conditions, including I-SES ($n = 8$) or C-SES ($n = 8$). Participants were not permitted to participate in both study conditions to minimize radiation exposure from videofluoroscopy and to avoid carry-over effects between sessions. All participants were naive to the study design. In both I-SES and C-SES, the pre- and postperturbation periods involved no stimulation.

Stimulation during the perturbation period. I-SES and C-SES conditions were different only during the perturbation period. During I-SES perturbation, stimulation was administered intermittently, that is, only during the swallows (immediately after the swallow cue until the hyolarynx returned to rest) but not during the 10-s interswallow intervals. Thus, while the investigator provided the swallow command, videofluoroscopy was watched for posterior lingual propulsion (propelling the water into the pharynx), and SES was delivered simultaneously with that event. During C-SES perturbation, stimulation was administered continually during both swallowing and interswallow intervals.

Postperturbation swallow. Previously, we masked perturbation removal by simply reducing the perturbation from a high-intensity, sensory-motor level that resisted hyolaryngeal elevation to a low-intensity, sensory-only level that did not perturb hyolaryngeal elevation (Humbert et al., 2013). The goal was to maintain sensory cues associated with the perturbation (SES tingling sensation) and, thereby, to mask the impending removal of the perturbation. As a result, participants demonstrated aftereffects and overshoot baseline peak hyolaryngeal elevation levels in anticipation of a perturbed swallow. In the current study, we aimed to determine whether the sensory information immediately preceding the postperturbation swallowing cue is necessary to induce aftereffects. Therefore, the postperturbation swallows in both groups were void of SES. All participants were unaware that the perturbation would be removed.

Kinematic Analysis

The investigators performing the kinematic analyses were blinded to the perturbation type. Data analysis included range of motion (peak extent of movement) of the hyoid bone and the larynx independently and LVC timing. For kinematic analysis of peak elevation, videofluoroscopic recordings were digitized using Peak Motus (Version 9.2; ViconPeak, 2005). The following points were located on each frame: the superior/posterior aspect of the subglottal air column (*y*-axis) to measure the position of the larynx and the anterior/inferior–most point of the hyoid bone (*y*-axis). Peak vertical hyolaryngeal movements were determined relative to the C4 vertebrae, which served as a stable reference point (Humbert, Lokhande, et al., 2012). The fourth cervical vertebra was also used to adjust for any whole-body movement during swallowing. Hyolaryngeal elevation contributes to LVC, which prevents airway invasion of ingested material (Fink, 1974; Fink & Demarest, 1978; Fink, Martin, & Rohrmann, 1979; Logemann et al., 1992). Thus, we also derived LVC timing measures that have been previously published (Macrae, Anderson, & Humbert, 2014). We measured the duration to LVC onset, which is defined as the duration between hyoid burst and first frame of LVC (hereafter referred to as DTLVC in this article). Hyoid burst occurs when the onset of upward and/or anterior movement of the hyoid bone becomes accelerated and is followed by continued elevation and anterior movement in a forward

loop before the hyoid returns to rest. We also measured the duration of LVC (dLVC), which is defined as the difference between first and last frames of LVC.

Statistical Analysis

The primary goal of this study was to determine whether hyolaryngeal movements adapt to perturbations. To examine adaptation during the perturbation period in I-SES and C-SES groups (return to preperturbation/systematic error reduction), a linear mixed effects model was used to estimate the effect of perturbation group across the 20 perturbation trials (SPSS, Version 19; Gelman & Hill, 2007). There was a fixed effect of group and a covariate of trial. In a separate mixed-effects model analysis, we compared the four phases within each perturbation type including preperturbation mean, early perturbation period (first three perturbation trials), late perturbation period (last three perturbation trials), and the postperturbation swallows. There was a fixed effect of phase. When fixed effects were significant, pairwise comparisons were Sidak corrected for multiple comparisons. To test reliability of measurement on 15% of the data, intraclass correlation coefficients were computed. The intraclass correlation coefficient represents the proportion of total variation (between-subjects variability and measurement variability) that may be attributed to between-subjects variability. Values near 1 suggest that nearly all variability is essentially biological, whereas values near 0 indicate that variability is primarily a result of measurement problems. Reliability was very good for laryngeal peak (.93), hyoid peak (.80), dLVC (.81), and DTLVC (.98).

Results

All participants tolerated the procedures well, without dropouts or adverse events.

Perturbation Effects at Rest and During the Early Perturbation Period

It is important to establish that the initial perturbation effects were similar between both groups prior to determining whether subsequent adaptation differed. At rest, perturbation effects (downward displacement of the hyoid and larynx) were equivalent between I-SES (larynx = $-5.9 \text{ mm} \pm 1.3 \text{ SE}$; hyoid = $-10.3 \text{ mm} \pm 1.8 \text{ SE}$) and C-SES (larynx = $-5.7 \pm 0.8 \text{ SE}$; hyoid = $-11.4 \text{ mm} \pm 1.2 \text{ SE}$). Compared to baseline, swallowing peak hyolaryngeal elevation during the first three perturbation trials (early perturbation) was significantly reduced in both the I-SES and the C-SES groups (see Table 1). For dLVC and DTLVC timing measures, no statistically significant differences were found between preperturbation and early perturbation periods (see Table 1). Thus, although peak elevation was significantly lower at the start of the perturbation phase, LVC timing was maintained in these healthy adults.

Table 1. Within-group pairwise comparisons for four phases of the study (preperturbation, early perturbation, late perturbation, postperturbation).

Measure	Comparison	I-SES					C-SES				
		<i>M</i> difference	Low 95% CI	High 95% CI	<i>df</i>	<i>p</i>	<i>M</i> difference	Low 95% CI	High 95% CI	<i>df</i>	<i>p</i>
HY	Preperturbation versus early perturbation	-13.69	-19.10	-8.23	124	< .001	-13.83	-17.70	-9.90	124	< .001
	Early perturbation versus late perturbation	1.72	-5.10	8.50	124	.985	7.16	2.30	12.01	124	.001
LY	Preperturbation versus postperturbation	-4.20	-12.90	4.46	124	.729	-2.45	-8.60	3.70	124	.879
	Preperturbation versus early perturbation	-7.90	-11.40	-4.50	124	< .001	-6.82	-9.06	-4.50	124	< .001
	Early perturbation versus late perturbation	1.10	-3.10	5.40	124	.997	4.50	1.70	7.20	124	< .001
	Preperturbation versus postperturbation	-2.70	-8.20	2.60	124	.683	-3.30	-6.80	0.26	124	.085
dLVC	Preperturbation versus early perturbation	-31.61	-1.32	64.68	125	.068	1.33	-1.60	4.20	122	.262
	Early perturbation versus late perturbation	64.35	23.63	105.60	125	< .001	-0.72	-2.80	1.30	122	.934
DTLVC	Preperturbation versus postperturbation	4.95	-48.51	56.76	125	1.000	-0.08	-2.70	2.60	122	1.000
	Preperturbation versus early perturbation	-13.86	-5.21	33.00	125	.285	-1.16	-2.70	0.45	122	.294
	Early perturbation versus late perturbation	-10.89	-33.00	9.90	125	.770	1.17	-0.91	3.10	122	.604
	Preperturbation versus postperturbation	13.53	-16.50	42.90	125	.799	-0.08	-2.60	2.40	122	1.000

Note. Statistically significant differences are in boldface. I-SES = intermittent surface electrical stimulation; C-SES = continuous surface electrical stimulation; CI = confidence interval; HY = hyoid; LY = larynx; dLVC = duration of laryngeal vestibule closure; DTLVC = duration between hyoid burst and first frame of laryngeal vestibule closure.

Gradual Return to Baseline Levels (Error Reduction) During Perturbation

Gradual return to baseline was significantly different between the two groups across the 20 trials for hyoid and laryngeal elevation (see Figure 2 and Table 2). Estimates of fixed effects showed that peak elevation gradually increased in the C-SES group for both the hyoid (0.5 mm per trial) and the larynx (0.2 mm per trial). Importantly, no trend toward baseline levels was observed within the I-SES condition. No dLVC timing trends were significant. However, during the I-SES perturbation, post hoc analysis revealed a significant increase in dLVC ($p < .001$), which increased by approximately 64 ms in late perturbation compared to early perturbation (see Table 1).

Aftereffects of the Postperturbation Swallow

Neither the I-SES nor the C-SES had significant aftereffects for any hyolaryngeal kinematic measure, because postperturbation swallows were not different from baseline swallows (see Table 1).

Discussion

The goal of this study was to determine whether the differences in perturbations cause variations in EBL. We focused on outcomes of systematic error reduction during the perturbation as well as aftereffects immediately after the perturbation was removed. We show that the context of the perturbation strongly influenced whether implicit learning occurred in swallowing hyolaryngeal kinematics.

Error Reduction and Its Neural Mechanisms

An important function of the human nervous system is to prevent harm and improve efficiency by reducing movement errors, which is partially achieved by feed-forward

control in EBL. The cerebellar cortex is a critical neural substrate of EBL (Wolpert, Miall, & Kawato, 1998). Albus and Marr theorized cerebellar contributions to EBL in two highly cited publications (Albus, 1971; Marr, 1969). In their model, the parallel fibers of the cerebellum (the excitatory fibers of the cerebellum) indicate the state of the body, including current motor commands. Unexpected events are detected by the climbing fibers that project to the Purkinje cells of the cerebellum. These neurons are important contributors to EBL for many sensory-motor systems (for a thorough review, see Taylor & Ivry, 2014). Thus, the cerebellum is a significant contributor to proprioception (awareness of body position), which is involved in evaluating the current body state relative to planned movements (Boisgontier & Swinnen, 2014). Peripherally, muscle spindles and cutaneous afferents (stretch receptors) all provide ascending sensory signals about proprioception to the cerebellum (Proske & Gandevia, 2009). Muscle spindles have been identified in intrinsic and extrinsic laryngeal muscles (Baken & Noback, 1971; Jakubowicz, Radziemski, & Kedzia, 1992; Larson, Sutton, & Lindeman, 1974). In our study, gradual error reduction during the perturbation may have been differentially induced when SES was administered to infrahyoid muscles. The C-SES perturbation may have sent consistent, reliable information to the cerebellum (possibly to cerebellar climbing fibers), allowing planning and execution of error reduction. As a result, feed-forward control may have led to increased activation of hyoid elevators (mylohyoid, geniohyoid, anterior and posterior bellies of the digastrics, hyoglossus) and laryngeal elevators (thyrohyoid, palatopharyngeus, stylopharyngeus) throughout the perturbation. Conversely, I-SES perturbation may have interrupted the error-reducing process of the cerebellum. Thus, commands to increase hyolaryngeal elevator activation may not have been sent or may have been sent inconsistently.

There may be more than one reason for differences in sensory input to the cerebellum. First, the presence of the

Figure 2. Peak movement of hyoid and larynx for intermittent surface electrical stimulation (I-SES) and continuous surface electrical stimulation (C-SES) conditions (in millimeters). Means of preperturbation swallows, 20 perturbation swallows (gray shaded region), and postperturbation swallows are shown. Error bars represent standard error.

perturbation during the interswallow intervals of the C-SES protocol might have established an expectation that the perturbation would also be present after the swallow command. Conversely, participants in the I-SES group experienced the perturbation sensation in close succession with the swallow command, leading to little time to plan to overcome the effects of the perturbation. Second, to participants in the I-SES groups had spontaneous, nonperturbed swallows during the interswallow interval approximately 55% of the time. Thus I-SES may not have promoted stable, predictable demands that are necessary to induce quick calibrations of hyolaryngeal

movements. In light of inconsistent demands, participants in the I-SES group did not learn to reduce errors during the perturbation block.

Aftereffects During Postperturbation Swallows

Neither group demonstrated aftereffects during the postperturbation period. We previously reported aftereffects when perturbation removal was masked with low-level SES that did not resist hyolaryngeal elevation (Humbert et al., 2013). However, it was not clear whether aftereffects occurred because sensory cues prompted participants to plan to swallow against the force of the perturbation in a feed-forward manner. The current study confirms that removal of those cues led to the absence of aftereffects. In the C-SES group, participants reduced effort to apply an appropriate amount of peak elevation necessary for an unperturbed swallow. The I-SES group did not learn to increase peaks during the perturbation period, so there was little expectation that aftereffects would be present.

Our findings are in line with other sensory-motor systems demonstrating varied learning outcomes in different perturbation contexts (Bingjie, Tong, Xinting, Jianmin, & Guijun, 2010; Dantas, Dodds, Massey, & Kern, 1989; Kim & McCullough, 2010; Tong & Flanagan, 2003). For instance, it has been shown that individuals can learn to overcome speech errors with one form of a perturbation, but not another (i.e., auditory vs. somatosensory perturbations; Schicatano, Mantzouranis, Peshori, Partin, & Evinger, 2002). In the limbs, the cerebellum responded more robustly to abrupt, continuous perturbations than varied perturbations (Schlerf et al., 2012). Overall, in many systems, it appears that predictable, continuous perturbations lead to larger EBL outcomes than less predictable perturbations (Criscimagna-Hemminger et al., 2010; Kagerer et al., 1997; Rand et al., 2004).

LVC

LVC is achieved with a combination of hyolaryngeal elevation and anterior movements, epiglottic inversion, and arytenoid adduction (Fink, 1974; Fink & Demarest, 1978; Fink et al., 1979; Logemann et al., 1992). LVC is multifaceted, requiring the coordination of several muscles (Seikel, King, & Drumright, 2010). It is notable that the early perturbation effects of hyolaryngeal elevation in I-SES and C-SES did not lead to changes in DTLVC or dLVC, perhaps

Table 2. Between-groups linear trend comparisons for the perturbation period.

Measure	Group by trial estimates	Estimate	Low 95% CI	High 95% CI	df	p
HY	Linear trend during perturbation	0.50	0.28	0.71	302	< .001
LY	Linear trend during perturbation	0.21	0.07	0.33	302	.002
dLVC	Linear trend during perturbation	3.63	-0.01	0.24	312	.070
DTLVC	Linear trend during perturbation	2.64	-10.89	4.95	312	.473

Note. Statistically significant differences are in boldface. CI = confidence interval; HY = hyoid; LY = larynx; dLVC = duration of laryngeal vestibule closure; DTLVC = duration between hyoid burst and first frame of laryngeal vestibule closure.

because this is a quickly adapting event that was already close to baseline behaviors within the first three perturbation trials that were measured (see Table 1). Furthermore, although C-SES peak hyolaryngeal elevation significantly changed across the perturbation period, neither DTLVC nor dLVC had a significant linear trend in any direction (see Table 2). However, in the I-SES group, dLVC significantly increased during the late perturbation period, compared to early perturbation, although no significant changes in peak hyolaryngeal elevation occurred during these same periods. All of these findings point to important avenues for future investigations of the LVC mechanism. First, it is possible that the primary goal of swallowing airway protection is to maintain adequate durations of LVC, despite changes in other related kinematics such as hyolaryngeal elevation. It suggests that hyolaryngeal peak elevation might accompany LVC, but may not be required to achieve adequate LVC under certain circumstances. Second, other events that may occur independent of hyolaryngeal elevation that we did not measure (i.e., epiglottic inversion, arytenoid kinematics) may have adapted to stabilize LVC. Third, it is possible that velocity of hyolaryngeal kinematics may be more important for LVC than range of motion (Nagy, Molfenter, Péladeau-Pigeon, Stokely, & Steele, 2014).

Potential for EBL in Dysphagia Rehabilitation

The potential and promise of applying the principles of motor learning to dysphagia rehabilitation have been asserted (Humbert & German, 2013; Macrae & Humbert, 2013). EBL is just one of many other forms of motor learning that need to be thoroughly explored for swallowing function. EBL has the potential to reveal how an intact swallowing system seamlessly adapts to numerous swallowing conditions (various foods, positions, changes in dentition) over short- and long-term periods. Importantly, when swallowing is disordered, EBL research paradigms may help to uncover whether impaired adaptation is a significant underlying pathophysiology. Our findings should be considered in patients with dysphagia who are being treated with SES on the neck. It is unknown whether these patients have intact EBL and can overcome the effects of the stimulation (perturbation) or whether they are unable to adapt, in any type of SES protocol (continuous or intermittent). Furthermore, EBL investigations in other systems show that patients with cerebellar infarcts adapt differently to different types of perturbations (Criscimagna-Hemminger et al., 2010; Lang & Bastian, 1999, 2001; Morton & Bastian, 2004). Given the role of the cerebellum in swallowing control, future studies of EBL are warranted and can contribute to dysphagia rehabilitation (Mosier & Bereznaya, 2001; Nagaya, Kachi, Yamada, & Sumi, 2004; Perie, Wajeman, Vivant, & St Guily, 1999; Prosiegel, Höling, Heintze, Wagner-Sonntag, & Wiseman, 2005). Furthermore, any concomitant effects on LVC have yet to be examined in patients who are being treated with SES.

Conclusions

We conclude that feed-forward control in EBL of swallowing hyolaryngeal elevation can be modified depending on the perturbation experience. Similar to adaptation in other behaviors, hyolaryngeal adaptation movements during swallowing were context specific. Our results are limited because they are derived from a healthy adult population without dysphagia. However, future studies are needed to determine how the principles of systematic error reduction can be incorporated into uncovering the basis of normal and abnormal swallowing airway protection. Understanding the circumstances under which learning and error reduction occur can offer important new insight into swallowing airway protection.

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