Differentiation of cerebral representation of occlusion and swallowing with fMRI

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Mihai PG, von Bohlen und Halbach O, Lotze M. Differentiation of cerebral representation of occlusion and swallowing with fMRI. Am J Physiol Gastrointest Liver Physiol 304: G847–G854, 2013. First published March 14, 2013; doi:10.1152/ajpgi.00456.2012.—Early work on representational specificity and recent findings on temporomandibular joint (TMJ) movement representation raise doubts that a specific swallow representation does exist. Additionally, during cortical stimulation TMJ movements and swallowing show a high overlap of representational areas in the primary motor cortex. It has thus been hypothesized that they overall might share the same neural structures. To differentiate these two movements, we performed a functional MRI (fMRI) study that enabled a direct comparison of functional representation of both actions in the same subject group. Effort during these tasks was controlled by skin conductance response. When balancing effort, we found a comparable neural representation pattern for both tasks but increased resources necessary to perform swallowing in direct comparison between tasks. For the first time, with the usage of fMRI, we demonstrated a representation in the brainstem for swallowing and occlusion. Increased activation for swallowing was observed in bilateral sensorimotor cortex, bilateral premotor and supplementary motor cortex, motor cingulate, thalamus, cerebellar hemispheres, left pallidum, bilateral pons, and midbrain. Peaks of activation in primary motor cortex between both conditions were about 5 mm adjacent. Brainstem activation was found corresponding to the sensory nucleus of the trigeminal nerve, the solitary nucleus for swallowing, and the trigeminal nucleus for occlusion. Our data suggest that cerebral representation of occlusion and swallowing are spatially widely overlapping, differing predominantly with respect to the quantity of neural resources involved. Both brainstem and primary motor representation differ in location with respect to somatotopy and contribution of cranial nerve nuclei.

swallowing; temporomandibular joint movements; occlusion; brainstem; functional magnetic resonance imaging; skin conductance response

TEMPOROMANDIBULAR JOINT (TMJ) movements and swallowing are both complex motor behaviors that are part of movement patterns necessary for food intake. TMJ movements are characterized by occlusion of the jaw to form masticatory actions to break down food for easier swallowing. They are usually of interest for investigation of neurophysiological or pathological representation of the jaw, for instance, to define the cerebral representation pattern associated with dysgnatia (36). Rhythmic muscle activity leading to TMJ movements are determined by a neuronal network known as central pattern generators (CPG) located in the brainstem (44). The ensemble of neurons involved is located in the vicinity of the trigeminal system, with the trigeminal nerve being the most important for TMJ movements together with its associated sensory, motor, and premotor nuclei (44).

When investigating occlusal movements in a blocked design, we found a representational map of primary and secondary motor areas, thalamus and cerebellar hemispheres, a frontoparietal network, bilateral insula, and cingulate cortex (37). Comparable to swallowing, a left hemispheric lateralization of bilateral occlusion of opercular areas to the dominant left hemisphere was reported (17, 37). Overall, representational sites described during occlusion seem to be widely congruent to those described during swallowing (30). Several decades ago, a “linguomandibular homotropy” was postulated, hypothesizing a functional overlap of swallowing and TMJ movements (61). Additionally, with respect to the primary motor cortex, direct cortical stimulation in man (16, 50) and animal (63) suggests an overlap of primary motor representational areas.

The functional representation of swallowing is widely investigated and clinically highly relevant (22). With respect to its cortical representation, the following representational sites have been described: bilateral inferior pre- and postcentral gyri (39, 59), bilateral anterior insula (25, 26, 51), anterior cingulate cortex (59), bilateral temporal pole, and the supplementary motor area (SMA) (23, 45). Opercular areas are lateralized to the left dominant hemisphere (40, 41). A time-shifted lateralization corresponding to the oral phase in the dominant hemisphere and the pharyngeal phase in the nondominant hemisphere is seen in an magnetoencephalography experiment (57). With respect to subcortical representational sites, the left cerebellum and dorsal brainstem have been reported, along with the basal ganglia (putamen and pallidum, Ref. 56) and the thalamus (39). Interestingly, the CPGs inferior to the fourth ventricle in the dorsal brainstem, which have been described to be crucially involved in reflective recruitment of swallowing in animal studies (10), were also observed to be activated during swallowing in a positron emission tomography study (23).

The common representational sights presented above led to the hypothesis that the activated regions of both tasks are overlapping. Furthermore, swallowing produces a greater cortical and subcortical activation compared with TMJ movements because the extent of movements involved in swallowing is more complex with respect to the interaction of muscles involved and movement patterns performed. The objective of our research was to qualitatively and quantitatively distinguish the cerebral activation of swallowing and occlusion using functional MRI (fMRI) with a special focus on automated processes in the brainstem.

Swallowing is composed of a coordinated sequence of motor activities with the help of sensory information to bring the...
bolus from the mouth to the esophagus. In contrast, occlusion consists of movement of the TMJ mainly involving four muscle pairs. The difference in complexity and coordination may lead to an increased effort during swallowing, especially in a supine position. Indeed, it has been described that the amplitude of skin conductance responses (SCR) is positively associated with effort (43). To control for possible differences in effort, we simultaneously measured SCR during fMRI scanning. We thus expect the SCR responses of swallowing in a supine position to be significantly higher than those during occlusion, in turn mirroring the blood oxygen level-dependent (BOLD) signal between conditions because swallowing is more exertive, requiring a more complex sensorimotor coordination.

MATERIALS AND METHODS

All procedures were approved by the Ethics Committee of the University of Greifswald (registration number BB 101/08).

Subjects. Twenty-one neurologically healthy volunteers [average age: 24.8 ± 3.2 yr (means ± SD); range: 20–33 yr, 16 female] participated in the study in return for monetary compensation. Informed, written consent was obtained before each study. All subjects reported no history of sensorimotor, swallowing, or cranio-mandibular pain conditions.

Tasks. Two functional, event-related imaging runs (duration 4 min, 20 s) were recorded during a single experimental session together with a structural T1-weighted high-resolution whole head data set. Subjects were instructed immediately before each task.

For the swallowing task, every 10 s, 2 ml (injection velocity: 2 ml/s) of room-temperature water was delivered through a soft rubber tube (diameter: 1.5 mm) 20 times using a MR-safe contrast agent injector (Spectris Solaris; Medrad, Warrendale, PA) (Fig. 1, top). Water was used because it does not provide a high degree of swallowing difficulty compared with saliva and is not as easy to swallow as a thicker fluid (25). The tube was held between the subject’s lips at midline. Water was delivered on a cued color change (blue to green) projected into the scanner as an ambient light. Subjects were instructed to swallow right after complete arrival of water. To control for swallowing timing, the movement of the pharynx was recorded with a pneumatic cushion. The pharynx exerts a pressure on the cushion attached to the neck. The cushion is thus squeezed, and the change in air pressure is transformed by a pressure detector into an electrical signal measured by an electro-optical biosignal recorder (Varioport-b; Becker Meditec, Karlsruhe, Germany). The pressure indicates the time of pharyngeal swallowing action. Subjects were instructed to swallow only when the full water volume arrived in the mouth and to avoid swallowing in between water delivery. As a result, reflexive swallowing was avoided and was verified by the pneumatic cushion signal, which recorded every swallow. If subjects suppressed the thought to swallow and waited for the next water delivery, the reflexive swallow became a volitional one.

For the TMJ movement task, subjects were instructed to perform three jaw-tapping movements within a 2-s period every 10 s on a cued color change as described above. A total of 20 repetitions per run was performed. A soft rubber tube was held between the upper and lower jaw like a bridle bit at the depth of the first or second premolars (Fig. 1, bottom). With the help of this tube, occlusal strength and frequency were measured through a pressure detector connected to an electro-optical biosignal recorder (Varioport-b; Becker Meditec). To reduce experimental complexity and to apply the same procedure in a patient population, sham stimuli were avoided.

Data acquisition. MRI data were collected using a 3 T MRI scanner (Siemens Verio, Erlangen, Germany) equipped with a 32-channel head coil. For each scanning session, field homogeneity was optimized by a shimming sequence, and a gradient echo sequence (34 phase and magnitude images, TR 488 ms, TE 1 4.92 ms, TE 2 7.38 ms, α = 60°) was acquired to calculate a field map aiming at correcting geometric distortions in the echo planar images. Echo planar images were measured during the two runs using the same field of view (FoV) as in the gradient echo sequence (TR 2 s, TE 22 ms, FoV 192 mm, slice spacing 2.5 mm, matrix 96 × 96, α = 90°, voxel size 2 × 2 × 2 mm³). The imaging volume was limited to one that encompasses brain areas involved in sensorimotor processing, cerebellum, and brainstem to obtain the highest possible resolution in the direction of the somatotopy. A total of 34 slices was acquired for each one of the 125 volumes recorded during one run. Additionally, a T1-weighted anatomical image was acquired (MPRage, TR 1690 ms, TE 2.52 ms, α = 90°, matrix 256 × 256, voxel size 1 × 1 × 1 mm³).

SCRs were measured during both trials from the distal phalanges of the index and middle fingers of the dominant hand using Ag/AgCl electrodes. Data were recorded using the BrainAmp MR system (Brain Products, Munich, Germany) with a gradient of 25 mV/μs, sampled at 5,000 Hz, and low-pass filtered with a cutoff frequency of 250 Hz. Units of skin conductance were recorded in microvolts.

Color changes were triggered with fMRI scans, and each color change sent a marker that was simultaneously recorded by the cushion pressure recorded as well as the SCR recorder. This ensured synchronization across multiple modalities without introduction of time lags. Pharyngeal movement recorded with the pressure cushion was analyzed with the cinematographic magnetic resonance sequence. The time of cushion compression coincided with the time of elevated pharynx. This instant was taken to be the end of the oral phase and beginning of the pharyngeal phase.

Data processing. Preprocessing and statistical analysis was performed with Statistical Parametric Mapping 8 (SPM8; Wellcome Department of Imaging Neuroscience, London, UK) running on MATLAB (MathWorks, Natick, MA). Echo planar images were spatially distorted echo planar images was performed in the phase-encoding direction with the help of a calculated field map. These images were then motion corrected and realigned to a mean image for each subject. Echo planar images were coregistered to the T1-weighted anatomical image. The structural T1 image was segmented into gray matter, white matter, and cerebro-spinal fluid maps. This segmentation was the basis for spatial normalization to the Montreal Neurological Institute (MNI) template. All echo planar images were smoothed with 6 × 6 ×
6 mm$^3$ full-width half-maximum Gaussian kernel filter to increase signal-to-noise ratio. Low-frequency components were filtered with a cutoff of 128 s.

Using BrainAmp Analyzer 2.0 (Brain Products), skin conductance data were artifact corrected, downsampled to 100 Hz, low-pass filtered with a cutoff frequency of 40 Hz, and exported to a MATLAB-compatible file. SCR was analyzed using the Ledalab toolkit (4) in MATLAB through a deconvolution approach. The signal was separated into tonic and phasic activity, followed by a trough-to-peak analysis on the latter, as described in Ref. 4. The mean SCR trough-to-peak amplitudes from the swallow and occlusion conditions were subjected to a paired $t$-test.

Statistical analysis. Event intervals between each trial were modeled with a boxcar function convolved with a canonical hemodynamic response function. The six movement parameters from the motion correction were used as regressors to account for coordinated movement artifacts. Individual statistical maps using the Student’s $t$-test were calculated for contrasts of interest: activation elicited by swallowing (swallowing), activation elicited by TMJ movements (occlusion), and comparison of activation (swallowing minus occlusion, occlusion minus swallowing). Statistical maps display location and intensity of activation of cortical and subcortical areas that are involved in swallowing or occlusion. The latter two differential contrasts test the overall difference between the two conditions to identify specific regions and activation strength between tasks. Contrast images for each were used in the group statistics calculated as a random-effects analysis at the second level, which takes the variance across subjects into account. The significance level for all contrasts was set to $P < 0.05$ family-wise error rate corrected for the whole brain volume.

Anatomical maps were defined using the Anatomy Toolbox (13) to describe location, intensity, and activated voxels in anatomical regions (Table 1). To assess distances in three dimensions between highest activated voxels in the primary motor cortex between swallowing and occlusion, Euclidean distances were calculated using the Pythagorean formula.

RESULTS

Swallowing latency from the visual cue to larynx movement was on average 2.6 ± 0.4 s (mean ± SD). This latency includes the water delivery time (1 s) and shows that subjects responded immediately after full arrival of the water volume. For the swallowing condition (Fig. 2A, Table 1, left), representational sites were found bilaterally in the primary motor and somatosensory cortex (M1), secondary somatosensory cortex (S2), premotor cortex (PMC), SMA, medial cingulate cortex (MCC), pars opercularis, insula, thalamus, cerebellar hemisphere, cerebellar vermis, pallidum, and pons.

For the occlusion condition, evaluation of performance data showed that the three taps had an average length of 1.5 ± 0.2 s. The same representational sites as during swallowing were found except for the SMA, left thalamus, right cerebellar hemisphere, cerebellar vermis, and left pons (Figs. 2 and 3, Table 1, middle).

When focusing on the somatotopic representation in the primary motor cortex, representational maxima during swallowing and occlusion were adjacent: for the left hemisphere the Euclidean distance between swallowing and occlusion was 4.5 mm and 4.9 mm for the right hemisphere. A closer analysis of the location of swallowing in the brainstem revealed activation in the principal sensory nucleus of the trigeminal nerve (MNI coordinates left: $-10, -30, -34$; coordinates right: $8, -26, -34$; Fig. 3). Additionally, activation of the solitary nucleus (MNI coordinates right: $4, -36, -44$) was found more caudal. The localization of the brainstem activation for the occlusion

<table>
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<th>Table 1. Coordinates of highest activation</th>
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<td><strong>Area (Brodman’s Area)</strong></td>
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<td>L M1 (BA 4)</td>
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<td>SMA ant (BA 6 medial)</td>
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<td>SMA post</td>
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<td>R Pars opercularis (BA 44)</td>
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<td>MCC</td>
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<tr>
<td>L Insula (BA 15)</td>
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<td>L Thalamus</td>
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<td>R Thalamus</td>
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<td>R Pons</td>
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<td>Midbrain</td>
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Statistical parametric mapping coordinates (Montreal Neurological Institute, x, y, z), $t$-values (T), and number of activated voxels per mask (k) of the highest activated voxel for the conditions swallowing, occlusion, and swallowing minus occlusion. All results are plotted for $P < 0.05$, family-wise error corrected. BA, Brodmann’s Area; L, left; R, right; ant, anterior; post, posterior; M1, primary motor cortex; S1, primary somatosensory cortex; S2, secondary somatosensory cortex; PMC, premotor cortex; SMA, supplementary motor area; MCC, medial cingulate cortex; CerHem, cerebellar hemisphere Larsell IV–VII.
condition was located more laterally in the trigeminal nerve and its nuclei (MNI coordinates: 16, −26, −34; Fig. 3).

The contrast swallowing minus occlusion showed significant activation in almost all areas reported for the main effect of swallowing except in the cerebellar vermis, right pallidum, and medulla (Table 1, right). The reverse contrast (occlusion minus swallowing) showed no significant voxels, underlining the increased cerebral and cerebellar resources necessary for the processing of swallowing.

SCR mean amplitude and standard deviation of trough-to-peak amplitudes across subjects were 0.079 ± 0.066 s for swallowing and 0.076 ± 0.056 s for occlusion. The paired t-test results of SCR data between conditions revealed no differences [swallowing minus occlusion: t(20) = 0.32, n.s.]. The data showed a drastic tonic change at the start of each scan accompanied by a few phasic peaks that were correlated with the onset light changes at the beginning, which subsequently diminished throughout the run (Fig. 4).

**DISCUSSION**

The objective of this experiment was to determine the difference in cerebral activation of swallowing compared with occlusion using fMRI. Furthermore, we controlled for possible differences of task effort using SCR measurements. Whereas previous fMRI studies have focused on the cortical areas involved in deglutition and occlusion, our study was aimed at subcortical processing networks, specifically at automated processes in the brainstem.

With respect to the areas involved, we found a common representational pattern of both tasks in the bilateral primary and secondary sensorimotor areas, the cerebellar hemispheres, the pallidum, the thalamus, and the insula. Functional representation in the precentral gyrus was represented as expected with representation maxima of swallowing inferior-anterior to those of occlusion. A completely new finding is a representation in the midbrain and the right pons, which was observed for both tasks, although different in location.

Brainstem activation for deglutition was found to correspond to the principal sensory nucleus of the trigeminal nerve and the nucleus tractus solitarius (NTS). Based on experiments done in sheep, a group of neurons at the level of the principal sensory trigeminal nucleus is classified as sensory relay neurons. These provide sensory information from the oropharyngeal receptors to the higher nervous centers and are not part of the swallowing CPG network (27). Microelectrode recordings performed on sheep, rat, dog, cat, and monkey place the NTS in the dorsal swallowing group as part of the brainstem swallowing neurons (1, 7, 9, 15, 28, 31, 35, 38, 46, 60). In humans, the cervical esophagus is composed of striated muscles that are innervated by the lower motor neurons. Peristalsis in this segment is due to sequential activation of the motor neurons in the nucleus ambiguous (19).

The brain stem swallowing network includes the NTS and nucleus ambiguus, with the reticular formation linking synaptically to cranial motoneuron pools bilaterally. Under normal function, the brain stem swallowing network receives descend-
ing inputs from the cerebral cortex (14). The NTS probably contains the second-order sensory neurons as well as the pattern-generating circuitry of both the pharyngeal and esophageal phases of swallowing (34). It recently has been proposed that water may constitute an independent taste modality and that somatosensory responses to water by water-dedicated neurons within the NTS may be part of neural circuits extending from the caudal NTS that produce ingestive reflexes such as swallowing (53).

Occlusional brainstem responses were localized more lateral in the trigeminal nerve (CN V) known to be most important for chewing (44). The Euclidian distance between the two activation maxima (swallowing and occlusion) on the right side was 8 mm. The occlusal CPG is primarily composed of neurons in the region of the trigeminal system (CN V) (44), whereas the swallowing CPG recruits the V, VII, XII motor nuclei, and the nucleus ambiguus (10).

Some recent results have indicated that interneurons localized in the dorsal or ventral regions of the swallowing network also fire during several motor behaviors, such as swallowing, respiration, mastication, and vocalization. The common motoneurons might therefore be triggered by common pools of interneurons. These results indicate that, in mammals, the neurons liable to be involved in pattern generation can belong to different CPGs (2, 7, 18, 32, 35, 47, 48, 62).

Brainstem activation for both tasks is most likely caused by the greater field strength of 3 Tesla, which increases the signal-to-noise ratio and contrasts to noise ratio, leading to an overall greater sensitivity (33). The small activation sites seen in the brainstem might also profit from high spatial resolution and low spatial smoothing used here (3).

The level of activation between both conditions differed substantially. Swallowing is a highly elaborate motor function requiring a coordination of a bilateral sequence of activation and inhibition among more than 25 pairs of muscles in the mouth, pharynx, larynx, and esophagus (8, 10, 29, 42). The sensory input provides feedback for proper bolus control. The contrast thus showed a cumulative activation of different sensory and motor biomechanical events, involving obligate muscles such as the geniohyoid, palatopharyngeus, and thyrohyoid muscles, the pharyngeal constrictors, muscles of the tongue and upper cervical esophagus (8, 11), and facultative ones such as tongue...
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muscles, facial muscles, and lip muscles (11). In contrast, occlusion is movement of one joint (TMJ) predominantly involving four muscle pairs. It comes as no surprise to see both a higher cerebral and cerebellar BOLD magnitude as well as a larger activated volume (9,400 voxels vs. 2,119 voxels) during the swallowing task as opposed to the occlusion task. However, an increase of effort was not verified by simultaneously conducted SCR measurements. Instead they depicted habituation responses over time, pointing to a novelty stress response to scanner noise rather than increased effort (65).

A significant lateralized response, as described by others for occlusion (17, 37) and for swallowing (57) was absent in our study for both tasks.

Areas found to be involved in both actions may not necessarily be task specific. In a “Go, No-Go” study of voluntary swallowing (59), cingulate cortex activation was attributed to processing of experimental context including task cues. Here, a change in color of the light used as a task cue for both swallowing and occlusion, as well as the injection of the water into the mouth, could cause the medial cingulate cortex to be activated. Furthermore, right insular activation found in both tasks may aid in the coordination of task performance (12). The difference in intensity ($t = 14.26$ for occlusion and $t = 10.25$ for swallowing, $P < 0.05$ family-wise error corrected) might be associated with heightened attention necessary for the counting of three occlusal movements right after the light changed color.

The simultaneous and congruent movement of tongue and jaw during mastication, e.g., when the jaw moves to the right so does the tongue, meaning they influence movements of each other, was described by Wild (61) as linguomandibular homotropy. Furthermore, experiments using intracortical microstimulation of the pericentral/perisylvian cortex (face-MS1, BA6 immediately lateral to face-M1) in awake monkeys evoked pharyngeal swallowing together with rhythmic jaw movements (24, 39a, 63). The authors thus suggest that certain cortical sites may integrate swallowing with TMJ movements. Functional MRI measurements during lip pursing, jaw clenching, and tongue rolling compared with swallowing of saliva show a high degree of similarity, suggesting a common processing network not specific to swallowing (30). These similarities encompass the regions of activity, the volume of activated voxels, and increases of signal intensity. A further point worth mentioning is that occlusion accompanies swallowing (49).

Limitations. Although we carefully optimized the setting in the scanner, applied realignment procedures, and used realign parameters as additional regressor, false-positive effects induced by motion, especially when synchronized with the task, cannot be excluded completely. Even if this motion is outside the FoV, an increase in signal intensity of the same order or above the percent signal change of the BOLD signal is induced in nearby tissue (64). Susceptibility artifacts in the static magnetic field caused by transition between different tissue types were made more uniform using a shimming sequence (21), and the resulting deformations in echo planar images were unwarped using a field map. Nevertheless, tissue motion during swallowing or occlusion causes dynamic changes in the static magnetic field, which cannot be accounted for by shimming or field map unwarping. Instead, the use of motion parameters in the model as regressors of no interest reduced the movement-correlated activation. Indeed, event-related experiments, such as the one described here, are less affected by motion artifacts (55), and, because the task occurs briefly, the motion can be separated from the BOLD response, which has a delay of 5–6 s (5). Nonetheless, these precautions offer no guarantee that brainstem activation is not a result of motion during swallowing and occlusion, especially because these actions are most prone to reveal motion artifacts in this region (55).

Brain stem neurons, in particular in the nucleus ambiguous organized to fire consecutively, produce a sequential excitation of esophageal muscles to provoke peristalsis (52, 58) lasting 10 or more seconds in conscious humans (20). This long-lasting excitation might induce a series of BOLD responses, which will overlap with ones from the proceeding swallow, confounding the signal. Nevertheless, an analysis in time using the hemodynamic response function model, as implemented in SPM8, showed activation in the brainstem timed with the actual swallowing task and not anywhere in between swallows. This temporally confined BOLD magnitude might be associated with the initial transport of oxygenated blood to the brainstem, which supplies enough oxygen to all sequentially organized cells responsible for peristalsis. Indeed, the amount of oxygen supplied greatly exceeds the one metabolized (6).

Conclusions. In conclusion, on a spatial resolution obtained here, cerebral representational areas of swallowing and occlusion showed a considerable overlap although the level of activation between conditions differed substantially. This finding gives rise to the idea that cerebral representations of both aspects of food intake are qualitatively widely overlapping but differ with respect to the quantity of neural resources involved. However, this increase of representational load is not associated with effort as controlled by peripheral physiology (SCR). Additionally, human brainstem fMRI activation for both swallowing and occlusion underlined results from previous animal studies and provided a new insight into subcortical processing of these tasks. In the brainstem, swallowing activated the sensory nucleus of the trigeminal nerve together with the solitary nucleus, whereas occlusion activated the trigeminal nerve (CN V), constituting a part of their individual CPGs.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS


REFERENCES


