Mastication is a three-stage process that prepares food for swallowing (Hiemae 2004; Morimoto et al. 1985; Schwartz et al. 1989). In the first stage, food is positioned and split into chewable pieces, preferentially between the anterior teeth. Tongue and cheek movements then transport the food to the occlusal surfaces of the molar teeth to be further divided by grinding actions. Finally, the food is gathered and transported to the pharyngeal region of the oral cavity and swallowed.

Central motor programs generate the coordinated pattern of orofacial muscle activation that underlies mastication (Lund 1991; Nakamura and Katakura 1995). This pattern is continuously modified via sensory feedback from intra-oral receptors to prevent and counter unpredictable events (Smith et al. 1985; Yamada and Haraguchi 1995) such as accidentally biting the oral tissues are most susceptible to damage (Lobbezoo et al. 2009; Lund and Olsson 1983). Reflexive jaw opening can also be elicited following nonnoxious stimuli such as a tooth tap or weak electrical stimulation of the oral mucosa (Lobbezoo et al. 2009; Lund and Olsson 1983; Sherrington 1917; Türker and Jenkins 2000; Yemm 1972). The response following nonnoxious stimuli is sensitive to movement phase but, in contrast to the protective jaw opening response, is largest when the jaw is in opening phase (Lobbezoo et al. 2009; Lund and Olsson 1983). Moreover, the nonnoxious response is sensitive to masticatory stage such that it is strongly suppressed throughout the preswallowing stage but not during the preparatory and grinding stages (Mostafeezur et al. 2009; Yamada and Haraguchi 1995; Yamamura et al. 1998). Reflexive jaw opening can also be modulated for different motor behaviors, such as rhythmic jaw closing and clenching, even when accounting for jaw gape and muscle state at the time of stimulation (Huck et al. 2005). Taken together, these studies show that reflexive jaw opening is modulated as a function of stimulus intensity, masticatory stage, movement phase, and motor behavior.

In the present study, we hypothesized that reflex responses in the digastic jaw-opening muscle are additionally sensitive to how a subject intends to bite through a food morsel. Such goal-dependent modulation has been shown for a wide range of muscles and is thought to underlie complex motor behaviors including reaching and grasping (Pruszynski and Scott 2012). Using a recently developed paradigm (Johansson et al. 2014), participants were asked to either split a peanut half stacked on top of a piece of chocolate without splitting the chocolate piece (i.e., single-split trial) or to split both the peanut-half and the chocolate in one biting motion (i.e., double-split trial). In both trial types, the unpredictable peanut split suddenly unloaded the jaw and evoked an rapid excitatory response in the digastic muscle (see for review Türker 2002). Consistent with our hypothesis, we found that splitting the peanut in the double-split trials evoked a smaller jaw-opening muscle response than the oral tissues are most susceptible to damage (Lobbezoo et al. 2009; Lund and Olsson 1983). Reflexive jaw opening can also be elicited following nonnoxious stimuli such as a tooth tap or weak electrical stimulation of the oral mucosa (Lobbezoo et al. 2009; Lund and Olsson 1983; Sherrington 1917; Türker and Jenkins 2000; Yemm 1972). The response following nonnoxious stimuli is sensitive to movement phase but, in contrast to the protective jaw opening response, is largest when the jaw is in opening phase (Lobbezoo et al. 2009; Lund and Olsson 1983). Moreover, the nonnoxious response is sensitive to masticatory stage such that it is strongly suppressed throughout the preswallowing stage but not during the preparatory and grinding stages (Mostafeezur et al. 2009; Yamada and Haraguchi 1995; Yamamura et al. 1998). Reflexive jaw opening can also be modulated for different motor behaviors, such as rhythmic jaw closing and clenching, even when accounting for jaw gape and muscle state at the time of stimulation (Huck et al. 2005). Taken together, these studies show that reflexive jaw opening is modulated as a function of stimulus intensity, masticatory stage, movement phase, and motor behavior.

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**METHODS**

**Participants.** Twelve healthy adults (21–29 yr; 5 men) participated in the study. All participants had normal dentition and relation between the jaws and gave their informed written consent. The study was approved by the local ethical committee and conformed to the Declaration of Helsinki.

**Apparatus.** Bite force and jaw position were measured with a custom-built device composed of an aluminum mouthpiece and a wooden headpiece (Fig. 1, A and B, respectively). The mouthpiece (Fig. 1A), weighing 26 g, consisted of a vertical beam (width × depth × height: 10 × 5 × 25 mm) to which two horizontal beams (width × length × height: 10 × 20 × 5 mm) were perpendicularly attached.

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The upper horizontal beam contained integrated strain gauges used to measure the bite force [0–1 kHz; range -10-150 N; root mean square (RMS) noise 0.006 N] and had a rectangular plate at the end on which the morsel stack rested. The lower horizontal beam was attached to the mandibular incisors by means of impression paste (PROVILE novo Putty Fast Set; Heraeus Kulzer, Wehrheim, Germany) applied in a milled pocket. To ensure that the impression paste between the edge of the mandibular incisors and the mouthpiece did not cause axial dampening, we visually confirmed that the tooth made contact with the bottom of the milled pocket. Once the paste had set, the participant could remove and replace the mouthpiece without assistance. By means of a screw coupling holding the lower beam to the vertical beam, the distance between the maxillary and mandibular incisors when the maxillary incisors contacted the morsel plate, termed bite height, could be set to either 11 or 16 mm. The stiffness of the mouthpiece in the direction of biting was 250 N/mm, and the unloaded resonance frequency of the system was 1.5 kHz. The wooden headpiece (Fig. 1B), fixed to the head by straps of hook-and-loop fabric, was used to measure the distance between the mandibular and maxillary incisors. This distance was measured by means of two three-axis magnetometers attached to the headpiece 170 mm apart (HMC2003 magnetic sensor hybrid; Honeywell, Plymouth, MN); they sensed the magnetic field of two cubic nickel-plated permanent magnets integrated in the mouthpiece (side 7 mm, NdFeB N42; Weibrecht, Göttingen, Germany). Because the two magnetometers were differentially influenced by the magnets of the mouthpiece but equally influenced by the Earth’s magnetic field, the distance between the upper and lower jaw could be calculated accurately regardless of the head position (0–1.5 kHz; range 60 mm; RMS noise 0.014 mm).

**Experimental procedures.** Before each trial, the participant manually held the mouthpiece and stacked a piece of chocolate and half a peanut (Estrella, Stockholm, Sweden) on the morsel plate. The rectangular chocolate pieces (6 x 15 mm) were cut from a solid chocolate bar (Baron Dark Chocolate; 70% cocoa, room temperature, ~5 mm thick). Importantly, the forces needed to split different peanut halves ranged from 15 to 45 N, thus making accurate prediction of the split event impossible (Johansson et al. 2014). The participant positioned the device in the mouth and contacted the mandibular incisors with their upper incisors with a self-selected force to control the morsel stack and the mouthpiece without hand support. After ~2 s, the experimenter asked the participant to perform either a single-split trial (“split the peanut without damaging the chocolate”) or a double-split trial (“split both the peanut and the chocolate in one action”). The participants performed 15–20 practice trials prior to data collection in which they learned to reload and place the mouthpiece with the morsel stack between their incisors. To test if the jaw opening muscle response was influenced by initial jaw opening, we performed the experiment in two blocks of trials with the bite height adjusted to 11 mm for one series and 16 mm for the other series (counterbalanced across subjects). Each block included 20 repeats of both trial types presented in pseudorandom order with no more than 4 repeats of the same trial type presented in a row. Trials were repeated if the peanut slipped or did not split cleanly during a trial (~10% of trials). After the experiment was completed, we excluded trials where the peanut was only partially fragmented or slipped off the chocolate. The final data set contained 367/480 (76%) single-split trials and 385/480 (80%) double-split trials.

**Data analysis.** Bite force was sampled at 2 kHz, and both position and EMG signals were sampled at 4 kHz, all with 16-bit resolution, using custom data acquisition software (SCZOOM; Physiology Section, Integrative Medical Biology, Umeå University). After the force signal was resampled to 4 kHz using linear interpolation, all data during the period covering 1 s before and after peanut split were exported to Matlab (The MathWorks, Natick, MA) for subsequent analysis.

Statistical analysis was performed using Statistica (StatSoft, Tulsa, OK). For analyses based on repeated-measures ANOVA, each measured variable was represented by its median value for each participant. Explained variance was averaged using the Fisher’s z transformation. Descriptive statistics are provided in the form of means ± SE. The statistical threshold was set at 0.05.
Experimental measures. Peanut and chocolate splitting was identified from the force rate signal obtained by symmetric differentiation of the force channel in a 4-ms window. The split event (see Fig. 1, C and D, dashed vertical line) was identified as the time of the local force rate minimum following a split, and the split force was measured as the maximum bite force preceding the split event.

Following jaw unloading after splitting of the peanut in single-split trials (and of the chocolate in double-split trials), there was a clearly observable increase in the bite force, representing the residual force (Fig. 1C; van Willigen et al. 1997) and, indirectly, the degree of dissipation of the jaw closing force. This residual force could not, however, be identified after the peanut split in the double-split trials because of the superimposed force increase applied by the participants to subsequently split the chocolate (Fig. 1D). For this reason, we defined an alternative measure, termed impact intensity, i.e., the peak rate in the force increase in a 30-ms time window following the split event. To minimize the influence of force transients introduced by small cracks in the morsel, the measurement was taken after low-pass filtering of the force rate signal (Butterworth, 3rd order, 30 Hz). For the single-split trials, the impact intensity correlated well with the peak residual force (r = 0.93), and the impact intensity could also be measured when unloading was followed by further increase of the bite force, since the peak across all participants occurred 17 ± 1.9 ms after the split event.

Final force rate just before the split event was defined as the average force increase during the 10-ms preceding the time of the identified split force. The hold force was defined as the force used by the participants to hold and control the morsel stack while awaiting instructions, and it was calculated as the mean force during a 150-ms window commencing 1 s before the split event. We defined the jaw travel during a split as the change in jaw position between the times of measurement of split force and impact intensity. Each EMG signal for each participant was rectified and normalized by its mean level over all trials in a 400-ms window centered on the peanut split event (Halaki and Ginn 2012). Thereafter, the EMG was low-pass filtered (2-pass Butterworth, 3rd order, 60 Hz). For the purposes of this study, the two samples of masseter muscle activity were averaged together (cf., Johansson et al. 2014). The results were qualitatively similar for a range of normalization and filtering parameters or when the masseter samples were considered in isolation.

The pre-split EMG level for both the masseter and digastric muscle was defined as the mean EMG value during a 40-ms window ending at the split event and was calculated for each trial and participant. On the basis of previous reports (Hanam et al. 1968; Lamarre and Lund 1975; Miles and Wilkinson 1982) and visual inspection of our own data (cf., Fig. 2A), we estimated the size of the jaw-opening response as the excitatory component in the digastric muscle following the split event. For each participant and each trial we calculated the jaw-opening response as the mean digastric EMG value above the digastric EMG pre-split value from the same trial in a 40-ms window commencing 20 ms after the split event (Fig. 2A, colored boxes in digastric EMG). Note that we were primarily interested in the excitatory component of the unloading reflex that is present on the digastric muscle involved in jaw opening. Although an unloading reflex is also present in the jaw-closing muscles (e.g., masseter and temporal muscle), this causes a strong inhibition, and therefore their early responses are difficult to quantify (Fig. 2A).

RESULTS

We present our results in three main sections. First, we analyze subject behavior while they performed the single-split and double-split biting tasks. Second, we directly test whether the jaw-opening response is modified by how the subject intended to bite through the morsel. Third, we analyze the relative influence of task and other parameters on the size and modulation of the jaw-opening response.

Subject behavior in the biting tasks. Each participant applied an idiosyncratic force (4.2 ± 2.7 N; mean ± SD of participant’s median; n = 12) to hold the morsel (i.e., a peanut half on top of a piece of chocolate) between their incisors. After receiving the instruction to perform either the single-split (Fig. 1C) or double-split trial (Fig. 1D), the participants increased...
masseter muscle activity and biting force. The task significantly affected the masseter muscle activity just before peanut split (Fig. 2B; \(F_{1,11} = 24.4, P < 0.001\)) and the final force rate (Fig. 2C; \(F_{1,11} = 80.1, P < 0.0001\)), but neither of these variables were modulated by bite height (\(P \geq 0.3\)). Similarly, there was no effect of bite height on pre-split digastric EMG (\(F_{1,11} = 2.6, P = 0.13\)), and the increase in averaged EMG levels in double-split trials compared with single-split trials did not reach statistical significance (\(F_{1,11} = 2.8, P = 0.12\)). The average split force was \(29 \pm 0.3\) N and did not differ significantly depending on either task (Fig. 2D; \(F_{1,11} = 3.14, P = 0.10\)) or bite height (\(F_{1,11} = 2.11, P = 0.17\)).

When the split occurred, the lower jaw moved toward occlusion and was halted when the upper incisors contacted the underlying chocolate. The impact intensity at contact was larger for the double-split task than for the single-split task (Fig. 2E; \(F_{1,11} = 38.4, P < 0.0001\)) but was not affected by bite height (\(F_{1,11} = 3.03, P = 0.11\)). The average jaw travel associated with the split of the peanut across the participants was \(3.4 \pm 0.4\) mm and was, on average, 0.6 mm greater in the double-split than in the single-split task (\(F_{1,11} = 4.07, P < 0.01\)). This small yet significant effect likely reflects a greater impression by the incisors on the chocolate in the double-split task caused by the stronger impact intensity. Bite height did not significantly influence jaw travel (\(F_{1,11} = 0.17, P = 0.96\)).

**Task-dependent modulation of the jaw unloading reflex.** The sudden force loss when the peanut split (i.e., the split event) evoked a jaw-opening response (Karkazis et al. 1993; Lamarre and Lund 1975; Miles and Wilkinson 1982; Yoshida 1998) that included transient inhibition of the masseter muscle (mean delay = 14 ms; Fig. 2A) and transient excitation of digastric muscle (mean delay = 16 ms; Fig. 2A). Both responses ended \(-60\) ms after the split event. Consistent with our hypothesis that the jaw-opening response is modulated as a function of stimulus intensity, bite height did not significantly influence jaw travel (\(F_{1,11} = 0.17, P = 0.96\)).

Factors influencing the jaw unloading reflex. The results reported above suggest that the effect of biting task on the jaw-opening response reflects task-dependent processing of sensory feedback. However, it is also possible that the participants modified other parameters of the biting action according to the instructed task and that these parameters, in turn, determine the magnitude of the jaw unloading response. For example, previous studies have shown that the magnitude of reflex responses to mechanical and electrical stimuli are sensitive to the level of preperturbation muscle activity (Bedingham and Tatton 1984; Marsden et al. 1976; Matthews 1980; Pruszynski et al. 2009; Verrier 1985). As such, the task-dependent modulation of the jaw-opening response may reflect systematic trial-by-trial changes in digastric muscle activation before the split event. It is important to emphasize that such correlations may exist even though we found no significant effect of either task or bite height on pre-split digastric muscle activation at the population levels.

We used a multiple linear regression model (full factorial, forward stepwise, \(P_{in} = 0.01;\) all data \(z\)-normalized) to predict the level of digastric reflex response as a function of task and other relevant parameters on a single-trial level. The model included two categorical predictors (task and bite height) and six continuous predictors (split force, final force rate, impact intensity, jaw travel, and mean EMG levels before split for masseter and digastric muscles). Figure 3 illustrates the principle finding of the modeling effort. The model accounted for 37% of the single-trial variance of the jaw-opening response (\(r^2 = 0.37; P < 0.001\)). Consistent with our hypothesis, the model revealed a significant main effect of task (\(P < 0.0001\)) in addition to main effects of digastric EMG before split (\(P < 0.0001\)) and split force (\(P < 0.002\)). We estimated the relative impact of the significant independent variables by means of partial \(\eta^2\) (Levine and Hullett 2002): task accounted for most variance (partial \(\eta^2 = 0.28\), followed by digastric EMG before split (partial \(\eta^2 = 0.05\)) and split force (partial \(\eta^2 = 0.01\)). In addition, we found three significant interactions, although these explained a relatively small fraction of the variance (partial \(\eta^2 = 0.01, 0.02, 0.01\); Table 1). Models generated for each subject individually performed well (average \(r^2 = 0.50\); range 0.19–0.85) and yielded similar results at the population-level model (10 of 12 showed main effect of task).

**DISCUSSION**

**Summary.** The main finding of this study is that reflexive jaw opening following sudden unloading of the jaw was modulated according to how the subject intended to bite through a food morsel. A larger response occurred when the subject was instructed to split one part of the morsel (i.e., the peanut) without damaging the other part of the morsel (i.e., the chocolate) compared with when they were instructed to split both parts of the morsel in a single action. Our results further those of previous studies showing that reflexive jaw-opening muscle response is modulated as a function of stimulus intensity,
Table 1. Model results across all participants

<table>
<thead>
<tr>
<th>Effect</th>
<th>F</th>
<th>P</th>
<th>Partial η²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Task</td>
<td>291</td>
<td>&lt;0.0001</td>
<td>0.28</td>
</tr>
<tr>
<td>Digastric EMG level before split</td>
<td>44</td>
<td>&lt;0.0001</td>
<td>0.05</td>
</tr>
<tr>
<td>Split force</td>
<td>10</td>
<td>&lt;0.0002</td>
<td>0.01</td>
</tr>
<tr>
<td>Task × split force</td>
<td>10</td>
<td>&lt;0.0002</td>
<td>0.01</td>
</tr>
<tr>
<td>Bite height × impact intensity</td>
<td>16</td>
<td>&lt;0.0001</td>
<td>0.02</td>
</tr>
<tr>
<td>Bite height × impact intensity × force rate</td>
<td>7</td>
<td>&lt;0.01</td>
<td>0.01</td>
</tr>
</tbody>
</table>

A full-factorial forward stepwise multiple linear regression model predicted the level of digastric reflex ($r^2 = 0.37; P < 0.001$; the $P$ value to both enter and remove individual variables was 0.01). The $F$-value, $P$-value, and relative impact (partial $\eta^2$) are given for the main effect and interactions of the significant parameters.

masticatory stage, movement phase, and motor behavior (Huck et al. 2005; Lobbezoo et al. 2009; Mostafeezur et al. 2009; Yamada and Haraguchi 1995; Yamamura et al. 1998). That is, we show that reflexive jaw opening was sensitive to the goal of biting even though the stimulus intensity, masticatory stage, movement phase, and motor behavior all were constant at two different bite heights.

We have studied reflexive jaw-opening muscle responses evoked by suddenly unloading the jaw when biting thru a morsel of food (i.e., the sudden unloading reflex reviewed in Türker 2002). To this end, we focused on the excitatory response of the digastric muscle because it has been claimed to be representative of the whole jaw-opening group (Ahlgren et al. 1978; Pancherz et al. 1986; Winneberg and Pancherz 1983) and because jaw-closing muscle activities are strongly inhibited and thus difficult to quantify. However, the full reflex response includes a distinct temporal arrangement of excitation and inhibition in many jaw-opening and jaw-closing muscles (Lamarre and Lund 1975; Miles and Wilkinson 1982; Yoshida 1998). That is, jaw-closing muscles are inhibited ∼15 ms after unloading (i.e., peanut split), and within a few additional milliseconds the jaw-opening muscles are also excited.

Behavioral consequences of task-dependent modulation. The single-split and double-split tasks were chosen because they require participants to differentially control the level of bite force following the unpredictable peanut split. That is, low bite forces following peanut split reduce the likelihood of splitting the chocolate piece, whereas high bite forces following peanut split increase the likelihood of splitting the chocolate piece. These functional demands were clearly reflected in the observed jaw-opening responses, which were larger in the single-split task than in the double-split task, consistent with the notion that jaw-opening responses following sudden unloading contribute to bite force development (Lund et al. 1983; Türker 2002; van der Glas et al. 2007).

From a mechanical point of view the optimal response in the double-split task is no jaw-opening response, because any such activity resists jaw closing. However, our data show that the jaw-opening response in the double-split task is not totally suppressed but is approximately half that seen in the single-split task. There are several reasonable explanations for the lack of complete suppression. First, it may reflect ambiguities of our experimental design such that the subjects were responding optimally given their understanding of our verbal instruction. Second, incomplete suppression may reflect a learning mechanism that operates on a time scale greater than that of our experiment such that participants could have eventually achieved no jaw-opening response given enough trials. Indeed, such limitations have been described for the human stretch reflex in various muscles (Wolf and Segal 1996; Wolpaw 1983; Wolpaw et al. 1983). Finally, incomplete suppression may be due to the fact that the digastric motor neurons are not actively hyperpolarized during jaw closing, and a peripherally evoked reflex activation of these would serve to increase the overall stiffness of the jaw system and support better contact and control of the morsel as it cracks (Goldberg et al. 1982; Proeschel and Raum 2003; Türker 2002; Yoshida 1998).

Mechanisms underlying task-dependent modulation. The observed task-dependent modulation of the jaw-opening response may have resulted from differences in muscle activity immediately before the split event. Indeed, previous studies in various motor systems (Capaday and Stein 1987; Houk et al. 1970; Kernell and Hultborn 1990; Marsden et al. 1976; Matthews 1986; Slot and Sinkjær 1994), including the jaw (Koutris et al. 2010; Lobbezoo et al. 1993), have shown that the same mechanical stimulus will elicit larger responses when pre-stimulus muscle activity is increased. This concept, termed gain-scaling, is generally attributed to the intrinsic organization of the motor neuron pool (Matthews 1986) where motor units are recruited in order of their force-generating capability and resilience to fatigue (Cope and Clark 1991; Henneman 1957).

Such an organization seems to be present in this context, because our trial-by-trial analysis revealed that a proportion of the jaw-opening response variance is accounted for by pre-split digastric muscle activity. Critically, however, we found no significant difference in pre-split digastric muscle activity between trial types, suggesting that the gain-scaling mechanism was not actively used to generate the task-dependent responses that we observed. Moreover, our ANOVA suggests a tendency for higher pre-split digastric activity in the double-split than in the single-split trials, and this tendency also can be seen in the principle finding of the regression model (see the rightward shift of red dots relative to blue dots in Fig. 3A), implying that any effect of gain-scaling works in the opposite direction from the effect of biting intention.

It is important to emphasize that the observed modulation of the jaw-opening response may rely on precise knowledge about the task. Since the peanut is the only element in the single-split trials and the first of two elements in the double-split trials, the observed modulation of the jaw-opening response may reflect the progression of the ongoing task. That is, the jaw-opening response may be small early in the biting action (i.e., after peanut split in the double-split trials) and large late in the biting action (i.e., after peanut split in the single-split trials). For example, reflex modulation has been described in a visuomotor reaching task where target position and movement speed were known and the reflex strength was modulated as a function of the distance to the spatial goal (Dimitriou et al. 2013). In the biting task we studied, however, the unpredictable bite force needed to split the peanut prevents such a predictive strategy. Ruling out such a scheme requires an experimental apparatus that, unlike ours, can systematically unload the jaw at various and unpredictable times.

Another possibility is that the observed modulation reflects a feedback control strategy that actively manipulates sensory information as a function of task. Indeed, task was a significant factor when analyzed at both the group and single-trial level. Given the short delay from the unpredictable split event to
reflex activation (~16 ms), it seems likely that the central nervous system instantiates the task settings before the split event and that the feedback control is mediated by relatively distal neural circuits. Almost all of the observed delay can in fact be explained by taking into account the peripheral sensory and motor conduction time (~3 ms each; Cruccu 1986; Cruccu et al. 1987), central conduction time (~3 ms both afferent and efferent), and disynaptic delays (~1 ms/synapse). The mechanism underlying the jaw-opening muscle activation thus appears to be different from those central mechanisms proposed to mediate task-dependent feedback responses in the limb motor system (Kimura et al. 2006; Pruszynski and Scott 2012; Shemmell et al. 2009).

The short delay from stimulus to motor response invites two speculative control paradigms. First, the response might be a preprogrammed motor act. In this case, given the time constraints, the central nervous system must preprogram and store motor commands within neurons at the brain stem level, likely within the trigeminal nucleus. To the best of our knowledge, such neural circuits have not been identified. In fact, data from animal models support an alternative, second control paradigm in which excitatory digastric premotor neurons within the trigeminal nucleus receive peripheral input and are subject to central modulation (Lund et al. 1983; Olsson and Westberg 1991). That is, the nervous system may set the sensitivity of these premotor neurons to sensory input and thereby the activity level of digastic motor neurons following peanut split.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS


REFERENCES


