Modulation of Jaw Muscle Spindle Discharge During Mastication in the Rabbit

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Masuda, Y., T. Morimoto, O. Hidaka, T. Kato, R. Matsuo, T. Inoue, M. Kobayashi, and A. Taylor. Modulation of jaw muscle spindle discharge during mastication in the rabbit. J. Neurophysiol. 77: 2227–2231, 1997. Discharges of jaw muscle spindles were recorded during chewing carrot from mesencephalic trigeminal nucleus (Mes V) in the awake rabbit to evaluate contribution of the muscle spindles to the development of complete sequences of masticatory movements. The Mes V spindle units were divided into two types according to the maximum firing rates during mastication, with a dividing line at 200 Hz; high-frequency units and low-frequency units. Although both types of units fired maximally during the jaw-opening phase of chewing cycles, their firing rates and pattern varied according to three sequential stages of mastication (stages I, IIa, and IIb). The high-frequency units often increased firing before the start of mastication and built up firing in the first few chewing cycles. Their maximal firing rate was sometimes lower during stage IIa (chewing stage) than during stage I (ingestion stage) and stage IIb (preswallowing stage), although the jaw movements were greater in stage IIa than in other stages. The phase relationship of the firing to a jaw movement cycle in stage IIa was consistent in individual units. The low-frequency units did not build up activity before the onset of movements. They fired mostly during the jaw-opening phase, but the peak of firing did not necessarily coincide with the time of maximal opening. It was concluded that the difference in the firing pattern among masticatory stages may be ascribed to a stage-dependent modulation of both fusimotor activity and jaw movement pattern.

INTRODUCTION

Mastication, like respiration and locomotion, is an example of rhythmic somatic motor activity originating in a central pattern generator. Its special feature is that it occurs in episodes each commencing with ingestion and ending with swallowing. The progress of mastication must be particularly dependent on the interaction of the motor mechanism with the variable load represented by the food. Because the size and consistency of the food bolus and its position relative to the teeth are all essentially unpredictable, it must be important for the action of the central pattern generator to be subject to control from peripheral sensory receptors. Mastication progresses through three recognized stages in the rabbit (Morimoto et al. 1985; Schwartz et al. 1989), and this orderly sequence must also depend on sensory cues. The muscle spindles in the jaw-closing muscles are likely to be important sources of the necessary sensory input, and this is confirmed by the observation that rabbits deprived of jaw muscle spindles have difficulty in controlling jaw-closing muscle activity (Morimoto et al. 1989). Various studies have been reported of the discharge patterns of the jaw spindle afferents during chewing and lapping in the cat (Cody et al. 1975; Taylor and Davey 1968), monkey (Goodwin and Luschei 1975; Matsunami and Kubota 1972), and rat (Yamamoto et al. 1989). In these studies the discharge patterns were analyzed for a particular stage but not for the whole of the masticatory sequence. However, more data are needed to understand how the muscle spindles contribute to the development of complete sequences of masticatory movements and to interpret spindle behavior in terms of the underlying patterns of fusimotor activity. This may now be undertaken with more confidence arising from recent expansion of knowledge of spindle physiology. In the present study advantage has been taken of the reliability of the rabbit for generating consistent sequences of masticatory movements and the facility of recording from the jaw-closing spindle afferents in the mesencephalic trigeminal nucleus (Mes V) in the awake animal.

METHODS

Ten male rabbits (2.3–3.0 kg) were used. All surgical procedures were reviewed and approved by the Osaka University Faculty of Dentistry Intramural Animal Care and Use Committee. The animals were anesthetized with α-chloralose (60 mg/kg) and urethane (500 mg/kg) via an ear vein. During surgery, anesthesia was maintained at such a level that no reflex jaw opening resulted from pinching the facial skin. The procedures for attachment of a phototransistor array to the mandible for tracing jaw movements and insertion of pairs of enamel-coated copper wires (150 μm diam, 5-mm spacing, 1.5-mm tip bared) into the left masseter and digastic muscles for electromyographic recording were the same as those reported elsewhere (Morimoto et al. 1989). A modified Evarts-type micromanipulator was fixed at the left occipital area for recording muscle spindle units in Mes V. The rabbits were maintained in good health by veterinary care throughout the experimental period. Recordings were started ≥4 days after the surgery and lasted several days (each daily session lasted ~2 h). During experiments the animal’s head was supported in a frame by means of the skull screws. Rabbits readily accept this type of fixation and chewed food without apparent disturbance. A glass-coated metal microelectrode with impedance of 1–3 MΩ at 1 kHz was inserted vertically through the left cerebral cortex toward Mes V. Four pieces of carrot that were cut as quadrangular prisms (3.5 × 10 mm) were inserted at a time into the animal’s mouth. Once we had succeeded in recording a unit discharge during mastication in a rabbit, the recording sites were marked by passing a negative current of 30 μA through the recording electrode for 10 s under deep anesthesia at the end of experiments. The animal...
was perfused with saline followed by Formalin (10%). In short, recordings and marking were performed by means of the one electrode in one animal. The recording sites were later identified on 50-μm sections of the brain stained with cresyl violet. The data were stored on a digital tape recorder, and later spike discrimination and data processing were performed by means of a NEC-Medicals DP-1300 computer.

RESULTS

The masticatory sequence was confirmed to be divided into three stages (I, IIa, and IIb) as reported previously (Morimoto et al. 1985), and the movement traces on the frontal plane at each stage are shown in Figs. 1A and 2A. Although >200 stretch-sensitive units were recorded in and around Mes V, only 18 units were successfully recorded throughout the whole masticatory sequence. These 18 units were identified as muscle spindle afferents, dependent on 1) the histological identification of the units in Mes V, 2) a low threshold to passive jaw opening, and 3) firing rates >100 Hz during mastication. Furthermore, for the masseteric units we confirmed the response to gentle probing of the masseter surface (see Cody et al. 1972; Kolta et al. 1990). They were classified into two groups according to the maximum firing rates during mastication, with a dividing line at 200 Hz (Cody et al. 1975): “high-frequency units” (14 units) and “low-frequency units” (4 units). The maximum instantaneous frequency averaged during 10 similar movement cycles at stage IIa ranged from 214 to 462 Hz (342 ± 86 Hz, mean ± SD) for the high-frequency units and from 107 to 181 Hz (141 ± 32 Hz, mean ± SD) for the low-frequency units.

Figure 1A shows an example of a high-frequency unit that responded to gentle probing of the anterior part of the left masseter muscle. It fired spontaneously at ~40 Hz, but began to increase 100 ms before the onset of mastication. Detailed examination in Fig. 1B shows that the first increase in frequency coincides with a small, slow horizontal movement of the mandible to the right and a very small opening, but is much greater than might be expected to be caused by the jaw movements alone (see Fig. 1C). Buildup of the afferent firing at the onset of jaw movements was observed for 10 of the 14 high-frequency units. When the main phasic jaw movements commenced during stage I, the discharge reached 400 Hz during the rapid opening and fell to zero during the closing phases, but the relation of the discharge to the movements was not constant. In stage IIa, the unit fired mainly during the jaw-opening phase and ceased or decreased firing during the jaw-closing and power phases (Fig. 1C). Two peaks appeared during the opening phase: one at the beginning and the other just before the maximum opening (Fig. 1, C and E). The maximum firing rate was between 250 and 400 Hz, that is, generally lower than that recorded during stage I. Of the high-frequency units, 10 showed this type of behavior. Three units fired throughout the masticatory cycles, but more strongly during the closing or power phases than during the opening phase. The one remaining unit showed an increase during mastication, but no clear modulation in relation to the movements. In stage IIb, the swallowing preparatory stage, the firing reached the peak at the beginning of the jaw-opening phase and its frequency was often higher than that recorded at stage IIa, although the jaw movement cycles slowed down (Fig. 1D).

One example from the four low-frequency units is shown in Fig. 2. In this case the spindle was not located in the masseter and had a spontaneous discharge at ~20 Hz. At the start of stage I, the firing rate gradually built up with the extent of the vertical opening movement. The rhythmic modulation was much less marked than in the case of the high-frequency units. The phase relationship of this unit’s firing was specific: the rate increased during the closing phase during the first few cycles, but changed to an increase during the opening phase thereafter (Fig. 2B). In stage IIa this low-frequency unit showed a constant phase relationship with activity extending from the middle to the end of the power phase, but was silent during the main closing phase (Fig. 2C). The firing rate showed two peaks, one at the onset of jaw opening and the other at the middle of the same phase (Fig. 2E). The maximum rate of 150–180 Hz occurred during the latter peak. In stage IIb the maximum firing rate was lower than in stage IIa (Fig. 2, A and D). Discharge patterns of the other three low-frequency units recorded were similar to the above, except that one was very insensitive to the small degree of opening at the beginning of stage I.

We compared statistically the position and velocity sensitivities of the muscle spindle afferents to jaw opening in the three stages. The position sensitivity was obtained by dividing the mean frequency during the jaw-opening phase by the maximum gape. The velocity sensitivity was obtained by dividing the mean frequency during the jaw-opening phase by the maximum velocity of the vertical jaw opening, which was evaluated as a differential of the jaw movement. Data were compared by analysis of variance (ANOVA) with repeated measures ANOVA and paired t-tests. Differences between variables were defined as significant if P < 0.05. Table 1 shows the results. Only the velocity sensitivities for the high-frequency units were significantly different among the stages (P = 3.76, P < 0.05). The velocity sensitivity of the stage IIa was significantly lower than either that of stage I (P = 3.70, P < 0.05) or that of stage IIb (P = 2.41, P < 0.05). On the other hand, the position sensitivities were not significantly different among the stages for either the high-frequency or the low-frequency units.

DISCUSSION

Categorization as primary or secondary spindle afferents would be very desirable, but the use of conduction velocity is not at all reliable for jaw muscles (Inoue et al. 1981). In the study of Cody et al. (1975) in the cat it was found possible to divide spindle afferent units into low-frequency and high-frequency groups according to their maximum firing frequency recorded during mastication, with a dividing line at 200 Hz. The high-frequency units were more velocity sensitive and were thought likely to be primary afferents, whereas the low-frequency ones were considered to be secondary. A similar approach has been adopted here, but the resulting division into 4 low-frequency and 14 high-frequency units is very different from the approximately equal division reported in the cat. It would be important to extend the present observations by the use of succinylcholine to
The behavior of the high-frequency units may be summarized as follows: 1) most of them discharged spontaneously; 2) they often increased firing before the start of jaw movements; 3) the maximal firing rate was lower in stage IIa than in stages I and IIb, although the jaw movements were greater in the former than in the latter; 4) the phase relationship of the firing to a jaw movement cycle in stage IIa was consistent in individual units; and 5) the units usually fired only during the jaw-opening phases in stages I and IIb. The low-frequency units were also spontaneously active, but there was little sign of a buildup of activity before the onset of movements. They fired mostly during the jaw-opening phase, but the peak of firing did not necessarily coincide with the time of maximal opening. If the low-frequency units are secondary units, then their frequency buildup in stage I may imply gradually increasing static fusimotor discharges. The increase during the closing phases in the first few cycles implies that there is rhythmically increased static action during
these phases. Its later disappearance may indicate that much of the resistance to closing had been broken down by then.

Spindle discharge reflects a combination of the effects of movement and of static and dynamic fusimotor activity. It is therefore possible from the present data to arrive at some conclusions regarding the natural patterns of fusimotor firing during mastication. The presence of a resting discharge in most units of both types suggests that there is background tonic static fusimotor activity, because dynamic activity would generally only affect primary afferents. However, the buildup of activity as the animal prepared to accept food was most evident in the high-frequency units. If the identification of these as primary units is correct, then there must be an enhanced dynamic discharge at this time. This would agree with findings from studies of mastication in the cat (Appenteng et al. 1980; Gottlieb and Taylor 1983) and would account for the high phasic sensitivity of the afferents to movement during this stage. With the onset of stage IIa,
the peak firing during jaw opening often decreased despite the increase in amplitude of the movements. This could be explained by a reduction in dynamic drive, but it could also occur if there were a modulation of static fusimotor outflow approximately in parallel with the alpha-motor activity, which has been proposed from the cat studies (Taylor et al. 1995). This could also account for the persistence of firing into the power phase of stage IIa. In stage IIb, all recorded units fired only during the jaw-opening phase and its peak was attained at the beginning of the opening. This response may result from enhanced dynamic fusimotor activity as in stage I. Because swallowing was not recorded in the present study, the moment of swallowing could not be identified. However, the jaw movement pattern at the end of stage IIb in Fig. 1, which was associated with relatively large lateral shift of the jaw, resembled that of the terminal swallowing reported by McFarland and Lund (1993) (Fig. 2 of that report). Furthermore, the spindle discharges were greater during this process. It is thus possible that the fusimotor drive is enhanced more during swallowing than during the preswallowing stage. Although there have been reports suggesting the possibility of synaptic inputs directly affecting the Mes V cells (e.g., Kolta et al. 1990; Nomura et al. 1985), the functional importance of such inputs has not yet been analyzed enough to be able to say whether they may make an important contribution to the changes in spindle behavior described here. For the present, it is taken that the variability in behavior of the spindles in the different stages can be best explained in terms of fusimotor output.

Finally, the question arises as to the functional implications of such stage-dependent changes in spindle firing. It could be argued that the most demanding stage from the point of view of regulating appropriate contraction in the jaw-closing muscles is the power phase of stage IIa. The force that will be required to crush the food cannot be predicted reliably, and so a load-compensating function might be expected to be contributed by the spindles acting through the stretch reflex. The spindles could only perform this function effectively if the static fusimotor output were to increase during this phase, because what is needed is for the spindle discharge to increase above normal if closing does not proceed at the expected rate. Clear evidence has indeed been provided previously for modulation of the static fusimotor output appropriate for this function in cats (Taylor and Appenteng 1981). The present results from the rabbit are consistent with this function being a feature of mastication. It is concluded that the fusimotor activity is modified in a phase-dependent manner to induce jaw movements appropriate for each stage of a masticatory sequence.

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REFERENCES


\begin{table}
\centering
\caption{Position and velocity sensitivities during stages I, IIa, and IIb.}
\begin{tabular}{lccc}
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Stage & I & IIa & IIb \\
\hline
Position sensitivity, Hz/mm \\
High-frequency units & 20.55 ± 7.55 & 19.86 ± 6.07 & 23.87 ± 14.22 \\
Low-frequency units & 8.95 ± 1.56 & 9.78 ± 2.36 & 13.27 ± 6.45 \\
Velocitiesensitivity, Hz·mm⁻¹·s⁻¹ \\
High-frequency units & 1.98 ± 0.76 & 1.39 ± 0.51 & 1.93 ± 1.11 \\
Low-frequency units & 0.93 ± 0.23 & 0.60 ± 0.17 & 1.20 ± 0.80 \\
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