Spike-Triggered Average Effects in Arm and Shoulder Muscles from Monkey Pontomedullary Reticular Formation Neurons

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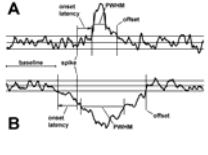
1. Abstract

Previous studies using stimulus-triggered averaging in the monkey pontomedullary reticular formation (PMRF) have revealed extensive bilateral reticulospinal outputs to arm and shoulder muscles. Forelimb stimulus-triggered averaging effects evoked from the monkey PMRF are similar to forelimb EMG response patterns evoked with stimulus trains in the cat PMRF; both response patterns are consistent with the PMRF contributing to the control of arm reaching movements. Anatomical and electrophysiological studies in the cat show reticulospinal neurons have monosynaptic projections to hind limb and forelimb motoneurons; however, there is little evidence for monosynaptic reticulospinal projections to monkey forelimb motoneurons. Here, we report spike-triggered averaging effects from PMRF neurons in arm, shoulder, and back muscles in monkeys performing a bilateral arm reaching task. Spike-triggered averaging effects were seen throughout the arm, including two wrist muscles, and were sometimes organized in reciprocal patterns between flexors and extensors. Some PMRF neurons produced spike-triggered averaging effects bilaterally. The onset latency and peak width at half-maximum of spike-triggered averaging effects from PMRF neurons covered a range indicating both pure and synchrony effects. These observations suggest that some monkey PMRF neurons may make monosynaptic connections to forelimb motoneurons.

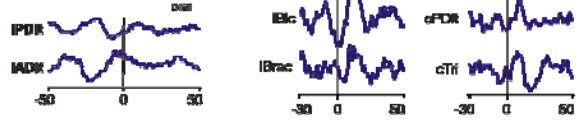
2. Methods

Four male *Macaca fascicularis* monkeys performed an instructed-delay arm reaching task as single neural-unit activity was recorded from the PMRF simultaneously with EMG activity in arm and shoulder muscles. Monkeys I and G reached with either the left or right arm to targets presented on a touch screen monitor; monkeys C and D performed a center-out planar reaching task with the right arm. Recording sites were ventral to the abducens nucleus, dorsal to the inferior olive and/or medullary pyramids, and medial to the facial nucleus (~ 4 mm lateral to the midline) and were confirmed with post-mortem anatomical reconstructions. For monkeys and I and G, EMG electrodes were implanted bilaterally in Flexor Carpi Radialis (FCR), Extensor carpi radialis (ECU), Brachioradialis (Brac), Biceps (Bic), Triceps (Tri), deltoids (anterior- ADlt; posterior- PDlt), Pectoralis Major (PMj), Lats (Lat), and the upper and middle trapezius (MTr, UTr). For monkeys C and D, Bic, Tri, PDlt, and Adlt were implanted ipsilaterally; the UTr and MTr were implanted bilaterally. In total, EMG data from 43 arm and shoulder muscles were analyzed with SpikeTA; 20 were ipsilateral, 23 were contralateral. Spike-triggered averages (SpikeTAs) were compiled off-line for each neuron-muscle pair. EMG was rectified and averaged over an 80 ms interval beginning 30 ms before the spike and ending 50 ms following the spike, smoothed with a five-point flat filter, and baseline ramps were removed by subtracting their slope from the final average. SpikeTAs were analyzed with multi-fragment statistical analysis (MFSA) (Poliakov and Schieber 1999), where the spike train was divided into smaller fragments to compile fragment SpikeTAs. EMG peaks (facilitation, Fac) or troughs (suppression, Spr) in the test period (3 ms to 15 ms) were considered SpikeTA effects when the test period EMG mean was significantly different ($p<0.05$) from the EMG mean of two flanking control periods (-8 ms to 3 ms; 15 ms to 27 ms) across all fragments. A neuron's SpikeTA effects were considered statistically significant if at least one neuron-muscle pair was significant after Bonferoni correction ($p< 0.003$). For each SpikeTA effect, we measured onset latency, peak width at half maximum (PWHM), and the peak and mean percent increase above baseline from onset to offset.



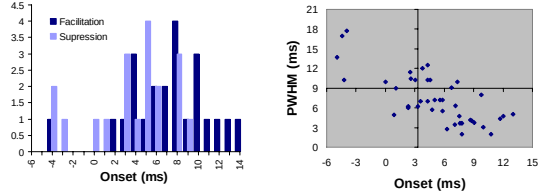
3. Single PMRF neurons produce SpikeTA Effects in muscles bilaterally

- 309 neurons were recorded throughout PMRF; 292 analyzed with SpikeTA, 3,968 neuron-muscles pairs
- 14 PMRF neurons produced 42 SpikeTA effects: 23 facilitation, 19 suppression
- On average, PMRF neurons produced a SpikeTA effect in 25% of the simultaneously recorded muscles
- 9 of the 14 neurons produced SpikeTA effects bilaterally: 28 ipsilateral, 14 contralateral
- Oscillations were present in the SpikeTAs of 5 PMRF neurons

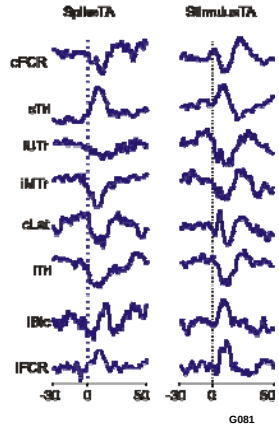


4. Temporal and amplitude characteristics of SpikeTA effects from the PMRF

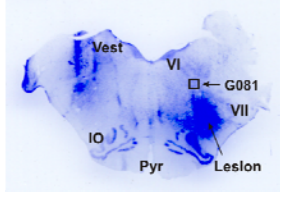
- The onset latency and peak width at half-maximum of SpikeTA effects from PMRF neurons covered a range suggestive of both pure and synchrony effects
- Mean onset latency was earlier for suppression (3.1 ms) than for facilitation (6.7 ms) ($p<0.01$)
- Mean PWHM was greater for suppression (9.0 ms) than for facilitation (6.0 ms) ($p<0.05$)
- No significant differences were found in SpikeTA effect amplitudes (PPI or MPI) comparing facilitatory vs. suppressive effects, ipsilateral vs. contralateral effects, or effects in various muscles



6. PMRF SpikeTA effects are similar to StimulusTA effects

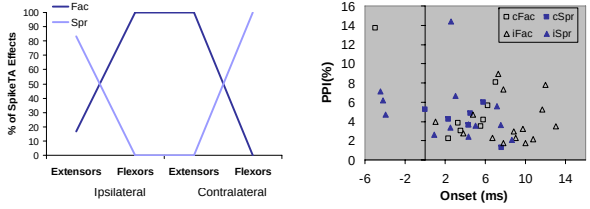


- Stimulus triggered averaging was attempted at 13 of the 14 sites where PMRF neurons produced SpikeTA effects
- These 13 PMRF neurons produced SpikeTA effects in a total of 39 neuron-muscle pairs.
- 27 of 39 (69%) SpikeTA effects had matching StimulusTA effects; 8 (21%) had no matching StimulusTA effect
- 4 of 39 (10%) SpikeTA effects were opposite in sign to the StimulusTA effect: all of which were SpikeTA effects in the upper trapezius (UTr)

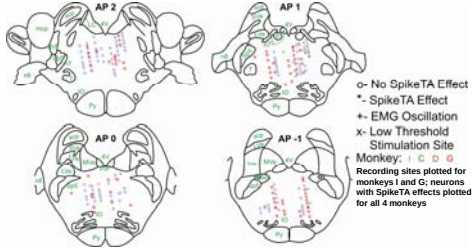


5. PMRF neurons produce reciprocal SpikeTA effects in the flexors and extensors of the arm and shoulder

- In general PMRF SpikeTA effects facilitated ipsilateral flexors and contralateral extensors; but suppressed ipsilateral extensors and contralateral flexors
- Only exception was iPdlt: 2 of 3 SpikeTA effects were facilitation
- Mean onset of ipsilateral suppression (2.6 ms) and contralateral facilitation (3.6 ms) was earlier than ipsilateral facilitation (8.3 ms) ($p<0.01$)
- Patterns of facilitation and suppression of shoulder girdle muscles--Lats, UTr, and MTr--varied



7. Similar spatial location of PMRF neurons producing SpikeTA effects



- We recorded neurons and performed StimulusTA throughout the PMRF (Davidson and Buford 2004; Davidson and Buford 2006)
- 15 neurons producing SpikeTA effects or spike-locked oscillations were recorded in a rostral-dorsal region (ventral to the abducens nucleus); 4 neurons recorded in a caudal-ventral region
- In rostral-dorsal region, low threshold stimulation often evoked large StimulusTA effects and single pulses of > 10 uA evoked visible twitches in shoulder muscles (Davidson and Buford 2006). This region appears to lie close to the site from which head movement can be elicited (Quessay and Freedman 2004; Cowie and Robinson 1984)

8. Conclusions

1. PMRF neurons produce SpikeTA effects bilaterally.
2. Onset latency and peak-width suggest a range of effects from pure to synchrony.
3. Some PMRF SpikeTA effects with early onset latencies may result from monosynaptic connections.
4. SpikeTA with PMRF neurons sometimes produced oscillations in the averaged EMG may reflect synchronization with cortical neurons.
5. The distribution (flexor/extensor, ipsi/contralateral, facilitation/suppression) of PMRF SpikeTA effects was similar to that of StimulusTA effects in our monkeys, and similar as well to movements evoked with repetitive stimulation in the cat PMRF (Drew and Rossignol 1984).
6. Most PMRF neurons producing SpikeTA effects were located in a limited region ventral to the abducens nucelus (NRGc). Other neurons were located rostral-ventrally (NRGm).

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