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## Neuronal activity of the supplementary motor area (SMA) during internally and externally triggered wrist movements

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The activity of neurones was recorded from the supplementary motor area (SMA) of monkeys while they were performing a discrete, arbitrary wrist movement. The cells responded similarly whether there was a triggering stimulus at the time of the movement or not. This experiment indicates that SMA neurones are active both in relation to externally triggered and internally initiated (voluntary) actions.

The supplementary motor cortex (SMA) is located on the medial surface of Brodmann's area 6. A number of suggestions as to its function have been made based on human experimental data [3, 9], neuronal activity in monkeys [5, 6, 10, 12, 13], and experiments involving lesions [1, 4, 8, 15]. In general, the investigators suggest that the SMA participates in some way in the initiation or coordination of learned, voluntary movements. We have restricted the definition of 'voluntary' to mean 'non-stimulus-evoked' and tested the hypothesis that the SMA is uniquely involved in the initiation of such movements. The hypothesis predicts that the SMA will be especially active during tasks which require initiation of actions in the absence of external stimuli. Therefore, we might expect to find SMA neurones which are more active during untriggered, 'voluntary' movements than during similar movements that are triggered by external cues. The following experiment was designed to determine if this was so. We have recorded from cells in the SMA of rhesus monkeys while they were performing a simple movement task. The task had two conditions, one in which a tone indicated that a movement could be made in order to obtain reward, and another in which there was no external triggering stimulus.

A recent paper by Romo and Schultz [10] also investigated the role of the SMA in voluntary movement. Their task required monkeys to reach into a box to retrieve a morsel of food. In our laboratory, we have found that monkeys with bilateral re-

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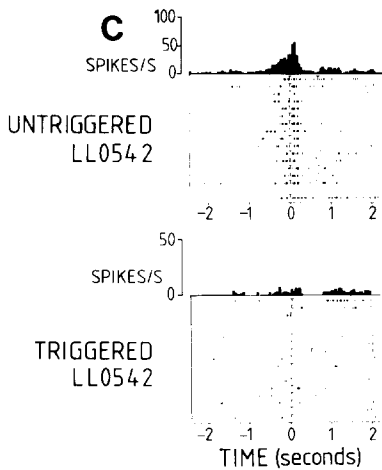
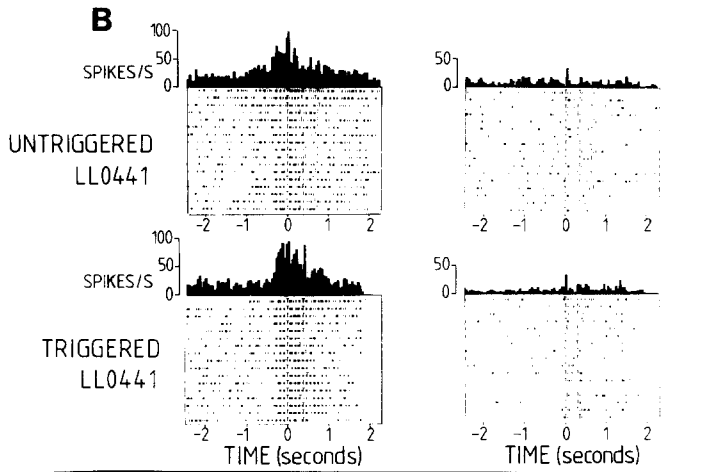
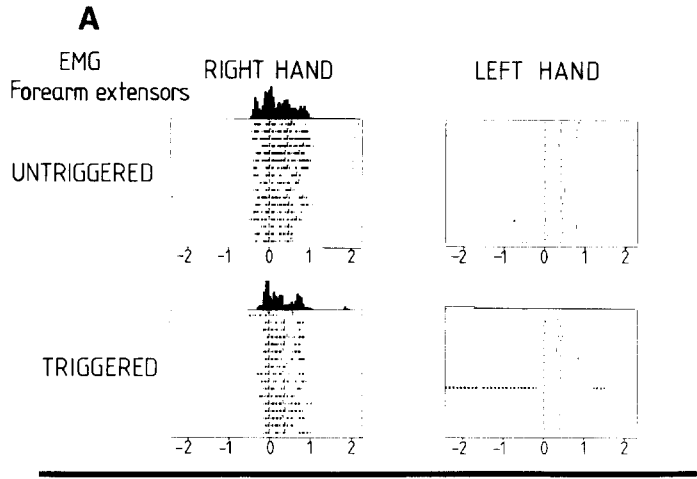
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removal of SMA are unaffected when the task involves reaching directly to the position where reward is found [15]. However, they are impaired at performing tasks in which they are asked to perform arbitrary movements (e.g. reaching an arm to break an infra-red beam) to obtain a peanut. In the present experiment we recorded from the SMA while the monkeys were performing an arbitrary movement. This paradigm then should be more sensitive and therefore more likely specifically to engage neuronal activity in the SMA than in previously reported recording studies [6, 7, 10]. In further distinction to some of these previous studies, the movement which we taught to our monkeys was a very closely defined wrist extension from a relaxed, flexed starting position. The earlier papers required the monkeys to perform whole arm movements which involve more muscle groups and postural adjustments and are therefore more difficult to measure accurately.

During the recording sessions the monkey sat behind a tube through which he could comfortably extend his arm so that his hand protruded through the other end. A closely defined wrist extension, starting from a relaxed, flexed position, was detected by the sequential interruption (within 250 ms) of a pair of horizontal infra-red beams placed 4 cm apart just beyond the end of the tube. In both conditions the monkey started a trial by keeping his hand in the lower beam throughout a hold period of random duration between 3 and 6 s. If the animal removed his hand, thereby reconnecting the beam, then the trial was aborted and the hold time reset. This hold procedure was identical for both conditions.

Reward (fruit juice) was available at the end of the waiting period and was delivered immediately after a successful response. In the triggered condition a tone (400 Hz, 0.5 s) came on signalling the end of the random length hold period. Therefore the tone acted as an imperative stimulus indicating that the delay was over and a response would then be appropriate. The other condition had no signal at the end of the delay and required that the animal initiate and execute his wrist extension without any relevant change in his sensory environment. A premature response was discouraged by the absence of the reward and restarting the hold timer. The aim was to train an identical movement differing only in the nature of the trigger. The movement in the first condition was triggered externally by the tone but in the second condition the monkey initiated the movement himself.

The different situations were presented in blocks of at least 17 trials. This means that after a few trials the animal knows whether his movement will require a signal or whether he will have to determine for himself when the movement will be appropriate. In an earlier design where the trials were mixed in random order [7], the animal was kept ignorant of the situation until the time at which the trigger ought to occur. It could be argued that in their design the monkeys may be responding to the absence of an anticipated signal. In fact, Tanji and Kurata already have discovered cells in the SMA that can be activated by just this type of missing stimulus [14]. Because of our design our monkeys were kept informed of the current demands of the task thereby circumventing the concern. Observations revealed that the animals performed the movement before the end of the hold period more often when they were initiating themselves than they did when waiting for an impending, expected tone.



We recorded from three hemispheres of two monkeys using standard electrophysiological techniques [11]. One monkey was equally proficient with both hands which allowed us to investigate the possible ipsilateral control of a cell which is active contralaterally. The monkeys were in the untriggered condition while the microelectrode was being advanced to the next neurone. If the neurone was unresponsive in this condition, it was abandoned immediately after recording its position. If it responded then formal testing and data collection were carried out to uncover inter-condition differences first with the hand contralateral to the cell then ipsilaterally. Note that this protocol would not allow us to find cells which were selective for the triggered condition alone or for cells which were only active on the side ipsilateral to the hand involved. Examples of the EMG recorded in the tasks are shown in Fig. 1A.

Our working hypothesis was that cells in the SMA would exhibit a greater response in the untriggered condition than in the triggered one but our data suggest that there is not a preponderance of neurones in the SMA which respond only or primarily in one of the conditions. Three hundred seventy-one cells were found in the SMA of which 81 (22%) were task related. Thirty-two of these 81 were sufficiently stable to allow the collection of data in both conditions for the contralateral hand. Of these 37 only two were more responsive in the untriggered situation. Twenty-seven (84%) of the cells responded like the one in Fig. 1B. They responded with a fixed relation to the active contralateral hand irrespective of the experimental situation in which they were being tested. One of these 30 cells, though, was strongly inhibited immediately prior to the movement. Note that the peri-response histograms are not aligned at the beginning of electromyographic activity but rather at the time the monkey removed his hand from the lower beam.

Only two neurones were found of the type we had predicted. Fig. 1C shows a cell which was active only in the non-triggered situation and which maintained its very low spontaneous rate of firing throughout the performance in the other condition.

Only two other types of neurone were found, also in very low proportions. Two cells responded in both conditions bilaterally though not as vigorously as those illustrated in Fig. 1. Finally, one cell increased its firing rate after the wrist extension though this was probably related to mouth or tongue movements during the receipt of reward.

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 Fig. 1. A: electromyographic recording taken from surface electrodes on the right forearm of the monkey. The right/left labels refer to the hand being used to perform the task. After being converted to a frequency measure (by triggering on spikes in the EMG), these recordings were collected and analyzed as if they were neuronal data. This figure demonstrates that the hand not involved with the task was fully relaxed and inactive in both conditions. The sole train of muscular activity in the left/triggered trial occurred when the animal used his right hand to scratch himself. It is also shown that the EMG in both conditions occurred discretely about the time of the movement. B: peri-response time histograms and data rasters for consecutive trials of a typical SMA neurone. Time 0 is the point at which the hand left the patch of the lower beam at the start of the movement. This neurone responded in both the triggered and the untriggered condition when the hand was contralateral to the recording hemisphere but was silent when the ipsilateral hand was being used. 1C. Peri-response time histograms and data rasters for consecutive trials of an SMA neurone which responded more in the Untriggered ('Voluntary') condition.

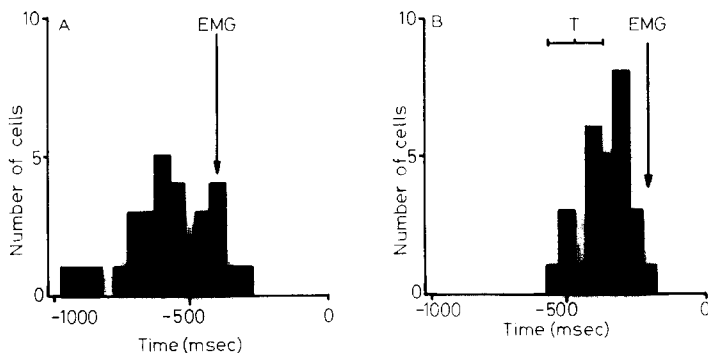


Fig. 2. Peri-response latencies of neuronal responses in the untriggered (A) and triggered (B) conditions. The latencies are in milliseconds relative to the detection of the movement. The mean reaction time is shown as T in the triggered condition (with a bar of one S.D.). EMG onset time is also indicated.

Therefore, most of the peri-response histograms were similar in pattern irrespective of the presence or absence of the auditory trigger. But there is some indication that the time course of active cells in the supplementary motor area differs between the two conditions which lends support to a similar recent finding [7]. The suggestion from our data is that in voluntary (non-stimulus evoked) movements, neuronal responses in the SMA appear earlier than during sensory triggered movements. The latency of the neuronal response was defined as the point at which the CUSUM [17] changed its slope. Fig. 2 illustrates the greater range of latency variability in the untriggered condition (mean =  $-567$  ms; S.D. =  $168$  ms) compared to the triggered trials (mean =  $-340$  ms; S.D. =  $95$  ms). It is possible that very slight muscular variations undetectable by our gross surface EMG recordings in the preparatory period are responsible for this difference. Indeed we did detect a more synchronous pattern of muscular activation in the triggered condition which may explain the greater alignment of cellular activation. Alternatively, this may be a true neural indication of different processing analogous to the conditions reflected in the human Bereitschaftspotential [3]. However, further research which is specifically designed for this possibility is required before the question is resolved.

Our findings thus show that SMA neurones respond in relation to both triggered and voluntary movements. In support of our finding, Romo and Schultz [1] report that in a small sample of cells ( $n = 13$ ) most of the neurones responded similarly during self-initiated and externally timed movements.

This experiment demonstrates that the SMA participates in movements which are well rehearsed and internally triggered (see also ref. 6). We have shown that neurones in the SMA also respond to an auditory triggering stimulus, and Tanji and Kurata [14] have shown that they respond to somatosensory and visual triggering stimuli. Therefore, these neurophysiological data show that SMA neurones participate in both stimulus-evoked and internally triggered movements and that their participation is comparable when movements are initiated in these different ways. We failed

to show a special participation of the SMA in internally *triggered* movements. Nevertheless, there are data from lesion studies that demonstrate that the SMA is involved in the performance of a certain class of voluntary movements [8, 15, 16]. The SMA lesions do not create impairments on the performance of externally-*instructed* movements but do on tasks which use internal *instructions*. In further neurophysiological studies it will be of interest to see whether a special involvement of the SMA neurones can be elicited by the performance of internally instructed movements.

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