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RESEARCH ARTICLE

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Pre-excitatory pause in frontal eye field responses

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Abstract We report a new characteristic of the presaccadic activity of the neurons in the frontal eye field of macaque monkeys. A fraction of neurons exhibited a significant pause in discharge rate preceding the excitatory visual or movement-related response. This pre-excitatory pause, which has been observed in striate and extrastriate visual areas, may represent a resetting of neural activation for detailed visual processing or saccade preparation.

Keywords Visual response · Visual latency · Suppression · Saccade · Visual processing

Introduction

The frontal eye field (FEF) participates in the transformation of visual computations into saccade commands (reviewed by Schall 1997; Schall and Thompson 1999). Several studies have related neural activity in FEF to perceptual and cognitive functions (see, for example, Bichot and Schall 1999; Bichot et al. 1996; Burman and Segraves 1994; Goldberg and Bushnell 1981; Kim and Shadlen 1999; Schall et al. 1995a; Thompson and Schall 1999, 2000; Thompson et al. 1996). However, we still have an incomplete understanding about the basic response properties of FEF neurons. We report a characteristic of FEF neurons that has not been described before – a pause in discharges immediately preceding the visual on-response or the presaccadic movement activation. This transient reduction of activity will be referred to as the *pre-excitatory pause* (PEP).

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Materials and methods

Subjects and surgery

Data were collected from three macaque monkeys (*Macaca mulatta* and *Macaca radiata*) weighing 4–10 kg. The animals were cared for in accordance with the National Institutes of Health for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care Committee. The surgical procedures have been described previously (Schall et al. 1995a).

Behavioral training and tasks

Using operant conditioning with positive reinforcement, the monkeys were trained to perform a countermanding task (Hanes et al. 1998) and a visual search task (Thompson et al. 1996). Two monkeys were trained to perform a countermanding task in which reward was contingent on either executing or withholding a saccade to a peripheral visual stimulus presented on a video monitor. All trials began with the presentation of a central fixation spot. After the monkey fixated this spot for a variable interval (500–800 ms), a target appeared at one of two locations, either in the most sensitive zone of the cell's response field or in the opposite hemifield at the same eccentricity. Simultaneously, the fixation spot disappeared, instructing the monkey to generate a saccade to the target. On 25, 33, or 50% of the trials after a delay the fixation spot reappeared, instructing the monkey to inhibit the movement initiation. During the trials in which the stop signal was not presented, monkeys were rewarded for generating a single saccade to the peripheral target within 700 ms and maintaining fixation on the target for 400 ms. During trials in which the stop signal was presented, monkeys were rewarded for maintaining fixation on the central spot for 700 ms after the target appeared. All three of the monkeys were trained to perform the visual search task. Each trial began when the monkey fixated a central spot. Following a specified interval, the target (for example, a red square) was presented at one of the eight positions around the central fixation spot and distracters (for example, green squares) appeared at the other seven positions with the same eccentricity. Monkeys were required to shift gaze to the singleton oddball stimulus. In separate testing monkeys produced memory-guided saccades to distinguish visually evoked from movement-related activity (Hikosaka and Wurtz 1983). Stimulus luminance was 10 or 30 cd/m^2.

Data analysis

Neurons were classified as visual, visuomovement, movement, and postsaccadic as described previously (Schall 1991). In this

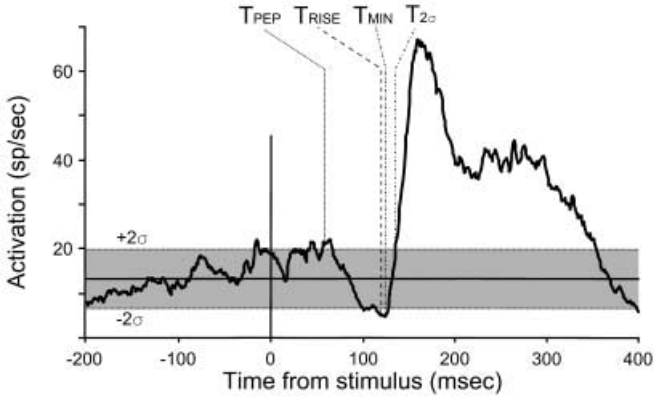


Fig. 1 Measures of neural modulation. The timecourse of activation of a frontal eye field (FEF) neuron is shown. *Gray strip* indicates level of activity bounded by ±2σ of the average firing rate during the period before the target appeared. T_{PEP} is the beginning of the decrease of activity preceding the excitatory response. T_{RISE} is the beginning of the monotonic increase in activation. T_{MIN} is the moment that the minimum of activation is reached. $T_{2\sigma}$ is the moment when the excitatory increase exceeded 2σ of the baseline

analysis, the visual cells and the visuomovement cells were combined. Postsaccadic cells were excluded from this analysis.

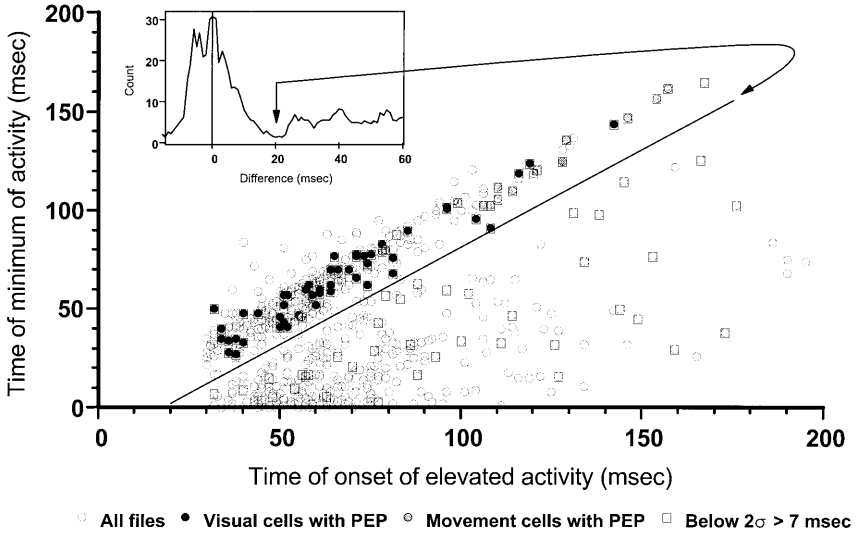
Spike density functions were constructed by convolving spike trains with a growth-decay exponential function that resembled a postsynaptic potential given by the equation $A(t)=(1-\exp(-t/\tau_g))\cdot(\exp(-t/\tau_d))$ where activation as a function of time [A(t)] varies according to τ_g, the time constant for the growth phase, and τ_d, the time constant for the decay phase. Based on measurements in the literature, we set τ_g=1 ms and τ_d=20 ms (Kim and Connors 1993; Mason et al. 1991; Sayer et al. 1990). The rationale for this approach, which has been described previously (Hanes and Schall 1996; Thompson et al. 1996), was to derive physiologically plausible spike density functions. Spike density functions were calculated from trials in which a correct saccade was produced to the target in the receptive field.

The measures used for the analysis are illustrated in Fig. 1. Baseline activity was the average value of the spike density function in the 200-ms period before the target appeared. The neuronal response was judged to be task-related if the activity exceeded two standard deviations above the baseline activity for more than 30 ms. Four specific times of modulation were measured on the spike density function. Two of the times were straightforward. We measured the time when the discharge rate exceeded the baseline firing rate by two standard deviations (referred to as $T_{2\sigma}$) and the time of the minimum of the activity occurring between target appearance and $T_{2\sigma}$ (referred to as T_{MIN}). We also measured the time when the activity began to increase before exceeding the threshold of two standard deviations above the baseline (referred to as T_{RISE}) using the following procedure. In a sliding window that was 40 ms wide, we determined whether successive spike density values over time were correlated according to a non-parametric Spearman rank-order test. Starting with the window centered on the $T_{2\sigma}$, the window was moved backward in 1-ms steps until the test became non-significant (P>0.01). The time of the center of the window producing the earliest significant positive correlation was defined as T_{RISE}. Because T_{RISE} was estimated using a window of finite size, while T_{MIN} was a single point, it could happen that $T_{RISE} < T_{MIN}$ (Fig. 1). This resulted in small measurement errors that did not change the conclusions. Neurons with T_{RISE}<30 ms were excluded from this analysis.

This algorithm was developed to find the time at which the activity of a neuron started to increase. Certain neurons in FEF, especially movement cells, exhibit activity that increases gradually. This situation is different from, for example, V1 where neurons have a rapid rise to the peak discharge rate (Maunsell and Gibson 1992). Hence, a measurement procedure was employed to define the onset time in two ways: the new measure (T_{RISE}) was complemented by a more conventional measure of activity onset ($T_{2\sigma}$).

The goal of this retrospective investigation was to determine whether FEF neurons exhibit a significant pause preceding the visually evoked or movement-related excitatory activation. The challenge was to distinguish a significant PEP from random fluctuations in firing rate. This was accomplished by analyzing the magnitude, duration, and timing of any decrease in activation occurring immediately before the growth of the visually evoked or movement-related activation. Three criteria were applied to classi-

Fig. 2 Timing of modulation. *Open circles* plot the relationship between the time when the activity reached its minimum (T_{MIN}) and the time when the activity began to increase (T_{RISE}) for every cell; individual cells could contribute more than one point if they provided sufficient data in more than one condition. If T_{MIN} coincided with T_{RISE}, then the points fell around the main diagonal. *Squares* enclose cases for which the discharge rate went below two standard deviations of the mean baseline firing for more than 7 ms, meeting the initial criteria for pre-excitatory pause (PEP). *Solid circles* mark visual cells and *gray circles* mark movement cells. *Inset* plots the distribution of the difference T_{RISE}–T_{MIN} exhibiting a clear minimum at 20 ms. The *diagonal line* marks the 20 ms division



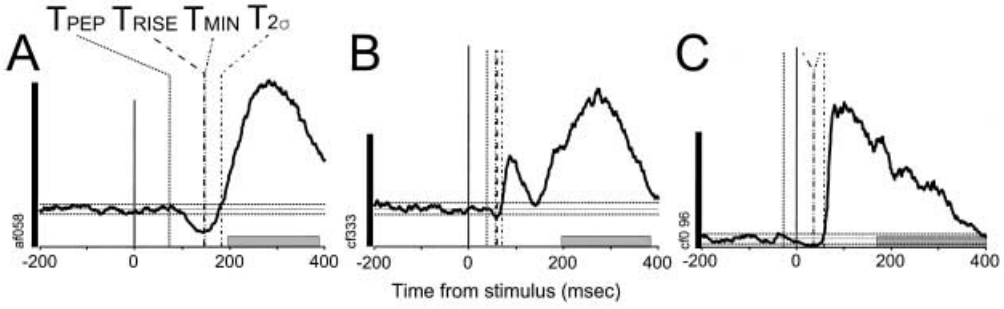


Fig. 3A–C Representative FEF neurons exhibiting PEP. **A** Movement-related neuron. **B** Visual neuron with visually evoked PEP. **C** Visual neuron with anticipatory PEP. Line conventions as in Fig. 1. *Vertical bar* indicates 100 spikes/s. *Gray horizontal* indicates range of saccade latencies

fy neurons as exhibiting the PEP. First, the level of the minimum of activity relative to the baseline was determined in units of standard deviation. Second, the period during which the activity remained below two standard deviations of the baseline was measured. Neurons with activity before the excitatory activation that fell more than two standard deviations below the baseline for at least 7 ms were candidates for exhibiting PEP. These criteria achieved the best balance between sensitivity and reliability. The third criterion was a requirement that the minimum of activity occur within 20 ms of the start of the major excitatory activation (T_{RISE}; Fig. 2). This criterion prevented the inclusion of spurious reductions of activity.

For neurons exhibiting a PEP, the onset of the pause (referred to as T_{PEP}) was defined using the same algorithm used to define T_{RISE}. This was the fourth measure of modulation. The window stepped backward in 1-ms intervals from T_{MIN}, and the time of the center of the window producing the earliest significant negative correlation was defined as T_{PEP}.

Results

Overall, 356 cells recorded from the rostral bank of the arcuate sulcus were analyzed. Of these, 172 (48%) were visual cells, 119 (33%) were visuomovement cells, 50 (14%) were cells with movement activity and little or no visual response, and 15 (4%) were cells with other classifications such as fixation or postsaccadic. This report will focus on neurons with visually evoked or movement-related activity.

The relationship between the time of the minimum discharge rate (T_{MIN}) and the time the activity began to grow (T_{RISE}) is illustrated in Fig. 2. Most of the cells which exhibited a pause in firing more than two standard deviations below the baseline lasting for more than 7 ms were clustered around the diagonal in the plot. However, the scatter plot reveals another distribution of points falling well below the main diagonal; these neurons exhibited T_{MIN} falling at no specific time before the start of the growth of activity. The distribution of T_{RISE}–T_{MIN} (Fig. 2 *inset*) exhibited a clear minimum at a difference of 20 ms, so this was selected as an effective partition between neurons with a difference between T_{RISE} and T_{MIN} sufficiently small to be interpretable as exhibiting PEP and the remainder for which T_{RISE} occurred at no particular time relative to T_{MIN}.

According to these criteria, 58 neurons in FEF exhibited PEP (16% of all cells tested): 22 were visual cells (38% of cells showing PEP, 13% of all visual cells), 21 were visuomovement cells (36% of cells showing PEP, 18% of all visuomovement cells), 13 were movement cells (22% of cells showing PEP, 26% of all movement cells), and 2 did not meet criteria for being classified in these categories. Thus, around 1 in 7 visually responsive cells exhibited PEP, whereas 1 in 4 of the movement cells in this sample exhibited PEP. Representative visual and movement cells exhibiting PEP are shown in Fig. 3. Visually evoked and movement-related PEP are distinguished in Fig. 2.

Of the cells exhibiting PEP, only eight had sufficient data collected in more than one task. Of these, five exhibited PEP before visually guided (detection or search) as well as memory-guided saccades, and two exhibited PEP before visually guided (detection or search) but not memory-guided saccades.

The times of the elevated activation ($T_{2\sigma}$) of all neurons and of the subpopulation exhibiting PEP were measured (Fig. 4). For all visually responsive cells the average latency (± SEM) of elevated activity was 74±1.1 ms. In contrast, the latency of the visually evoked activation for cells showing PEP was longer, averaging 91±3.5 ms (Fig. 4A). Similarly, the beginning of the monotonic rise in activity (T_{RISE}) for all visually responsive cells averaged 56±1.2 ms while for visually responsive cells exhibiting PEP it was 66±3.5 ms. Visually responsive neurons had an average PEP onset (T_{PEP}) of 23±3.9 ms (Fig. 4B). However, this average is so small because some neurons were identified with PEP beginning before stimulus presentation or too early to be visually evoked. The median PEP latency was 27 ms. The duration of PEP was defined as the difference between T_{PEP} and $T_{2\sigma}$. The duration of PEP for the visually responsive neurons averaged 61±3.2 ms (Fig. 4C).

For all movement-related neurons the growth of activation ($T_{2\sigma}$) occurred on average 101±4.9 ms after stimulus presentation. The onset of movement-related activity for cells showing PEP was 148±9.1 ms (Fig. 4A). The beginning of the monotonic rise in activity (T_{RISE}) for all movement-related activity averaged 84±4.4 ms while that for movement cells exhibiting PEP was 113±6.6 ms. Movement cells showed an average PEP onset (T_{PEP}) of 57±6.9 ms (Fig. 4B) with a median PEP latency of 61 ms. The PEP duration of movement-related neurons averaged 84±8.1 ms (Fig. 4C). Thus, T_{PEP} of visual cells tended to be earlier than T_{PEP} of movement cells, and PEP duration was slightly longer for movement cells.

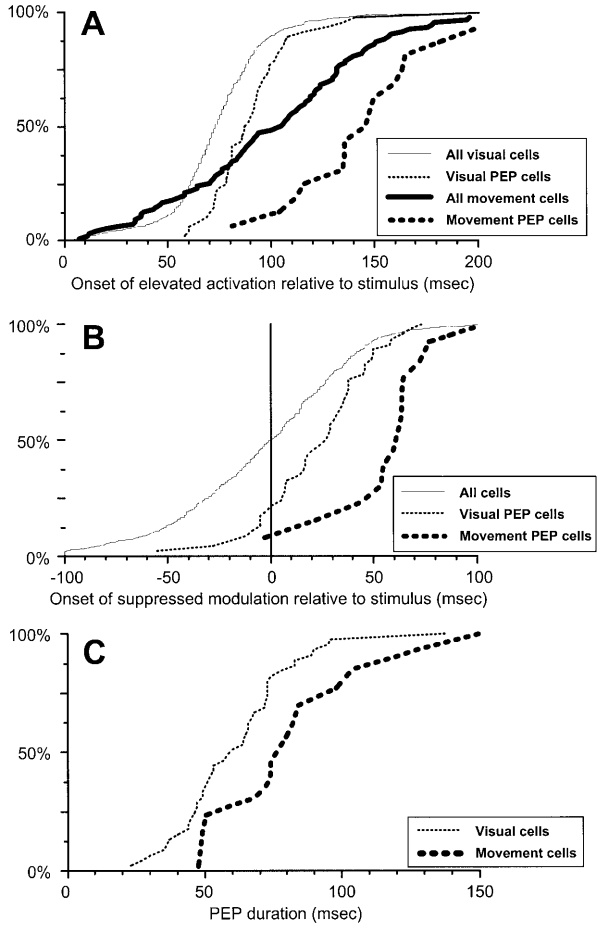


Fig. 4A–C Cumulative distributions of specific modulation times. **A** Onset of elevated activity ($T_{2\sigma}$) for the populations of neurons indicated in the key. The response latency of visual cells precedes that of movement cells. The response latency of cells exhibiting PEP is later than that of the population as a whole. **B** Onset of suppression (T_{PEP}) for the populations of neurons indicated in the key. In the overall population suppressed activity could occur over a broad range of times that were not synchronized on stimulus presentation. The suppression defined as PEP was more synchronized on stimulus presentation. **C** Duration of PEP for the populations indicated in the key

Discussion

We have described a new characteristic of the responses of a subpopulation of FEF neurons, a pause in activity that immediately preceded the excitatory activation in both visual cells and movement cells. We will relate the times of modulation we have observed to previous studies of visual latencies and discuss the possible origins and functional role of PEP.

A critical issue in evaluating this phenomenon is the reliability of the quantitative methods. One avenue of validation is to compare the latencies measured in this study with values reported previously. The visual response latencies measured in this study (average $T_{2\sigma}$=74 ms) were comparable to the latencies measured in FEF of anesthetized monkeys (average 75 ms; Schmolesky et al. 1998) and in the awake monkey (average 67 ms; Thompson et al. 1996) even though these previous studies used a different analytical method. Thus, the procedures used in this study to determine visual response times obtained values similar to those previously reported.

We now consider the reliability of the determination of the PEP. Any measurement procedure includes error. We sought to employ criteria that balanced sensitivity and reliability using converging evidence derived from separate measurements. One source of measurement error was introduced by the fact that T_{MIN} was a single point, but T_{RISE} required a finite size window (40 ms). This resulted in instances in which T_{MIN} followed T_{RISE}, but 50% of such aberrant values were within 5 ms and 80% were within 10 ms. Ultimately, in most cases the PEP identified by the algorithm could be seen clearly on visual inspection.

Further evidence for the existence of PEP is from reports of a modulation resembling what we have called PEP observed in studies of primary and extrastriate visual areas. An initial inhibitory response has been reported in area 17 of the cat (Borg-Graham et al. 1998; Creutzfeldt et al. 1969). An initial suppression was observed in the responses of 30% of neurons in V1 and V2 of macaques (Nowak et al. 1995). In a current source density analysis, an initial inhibitory response has been observed in area V4 and inferior temporal cortex but not in dorsal visual areas (Schroeder et al. 1998). In addition, modulation corresponding to PEP can be seen in other studies of ventral stream areas (for example, Fig. 8 of Desimone et al. 1984; Fig. 11 of Kovács et al. 1995; Fig. 3 of Richmond et al. 1983; Figs. 3 and 8 of Richmond et al. 1987; Fig. 2 of Sáry et al. 1993) and of prefrontal cortex (for example, Figs. 5 and 10 of Boch and Goldberg 1989; Fig. 3 of Funahashi et al. 1990; Fig. 8 of Mikami et al. 1982; Fig. 2 of Watanabe 1992). We conclude, therefore, that the modulation we call PEP is a real characteristic of signal transmission in the visual system.

How PEP arises in FEF is not clear. Both time and anatomy inform consideration of possible sources of PEP in FEF. One possibility is that PEP arrives in the cortical afferents to FEF (Schall et al. 1995b). Early studies of anatomical relations between visual cortical areas suggested that FEF is positioned rather high in a hierarchy of visual areas in the cerebral cortex, far removed from the retina (Felleman and Van Essen 1991; Hilgetag et al. 1996). However, FEF has been demoted in a recent study that concluded that FEF can provide feedforward activation to extrastriate visual cortex (Barone et al. 2000). Along the cortical pathway, the earliest visually evoked responses occur in striate cortex with latencies of 30–40 ms (Maunsell and Gibson 1992; Nowak et al. 1995; Schmolesky et al. 1998). The mean latency of the inhibitory response in V1 was 58 ms, and in V2 was 76 ms (Nowak et al. 1995). FEF is innervated directly by area MT and MST (Schall et al. 1995b) which receives major inputs from the fast magnocellular

pathway (Maunsell et al. 1990). In the only study to compare directly the visual response latencies of neurons in FEF with those of neurons in extrastriate visual cortex, the latency of neurons in FEF was 75±13 ms (min=51 ms), while that of neurons in area MT was 72±10 ms (min=49 ms) and in area MST was 74±16 ms (min=51 ms) (Schmolesky et al. 1998). The other possible source for PEP is the thalamic input to FEF arising primarily from the mediodorsal nucleus as well as the intralaminar nuclei (Huerta et al. 1986; Stanton et al. 1988). Visual latencies of cells in the mediodorsal nucleus are not known, and those in the intralaminar nuclei fell in the range of 77–135 ms (for 80% of units; Schlag and Schlag-Rey 1984). One of the major inputs to the thalamic nuclei innervating FEF is the superior colliculus (Lynch et al. 1994). Along the subcortical pathway, the earliest visually evoked responses occur in the superior colliculus with latencies of on average around 55 ms (min=40 ms; reviewed in Schall 1991). Neurons in FEF that are activated orthodromically through the thalamus by electrical stimulation of the superior colliculus were all visually responsive with one-half exhibiting movement-related activity (Sommer and Wurtz 1998). The mean latency of orthodromic stimulation of FEF from the superior colliculus was 2.7 ms. Thus, it is possible for visual activity to be conveyed to FEF from the superior colliculus through the thalamus with latencies as low as around 43 ms.

Based on these values, we can see that the PEP observed in the movement-related neurons could be of visual origin, but the PEP observed in many visually responsive neurons was too early to be visually evoked. Why did we find PEP occurring earlier than a visually evoked response? One possibility is a measurement error; this subtle modulation may be measured too early, so some of the PEP occurring apparently too early may actually be visually evoked. Still, measurement error cannot account for all of the early PEP. Therefore, we conclude that the PEP in many FEF neurons is visually evoked while the PEP in the remaining neurons is of extraretinal origin, making the two kinds of PEP possibly distinct phenomena although not necessarily subserving different functional roles. Observing extraretinal, anticipatory neural modulation in FEF related to predictable visual stimuli is not surprising. More than one laboratory has observed anticipatory visual responses in FEF (Bruce and Goldberg 1985; Schall 1991), and during a gap task movement neurons exhibit an anticipatory discharge prior to target presentation (Dias and Bruce 1994).

Because both corticocortical connections and thalamocortical connections are excitatory, there are two possible mechanisms for PEP. One is that the neurons that project to FEF also exhibit PEP. The other is that afferent neurons project to interneurons in FEF that produce the inhibition in another population of neurons that we observed as PEP. The second hypothesis seems difficult to accommodate in time, but further work is needed to decide between the alternatives.

What might PEP do? Of course, we do not know because we do not have sufficient or appropriate data. We prefer the working hypothesis that PEP is the signature that a component of the visual system is adopting a state appropriate for further processing (see also Nowak and Bullier 1997). We speculate that the transiently reduced firing rate may serve to increase the ratio of signal to noise in the subsequent elevation of activity or to reset an integrator. Clearly, additional research is necessary to ascertain the function of PEP, but this is certainly not the first nor only description of a characteristic of cortical neurons that has an unknown function. Moreover, such work on function is motivated by the existence of the phenomenon. The modest goal of this paper was simply to report this curious but common enough property of FEF neurons.

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