

The amplitude of elicited PGO waves: a correlate of orienting

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Summary Ponto-geniculo-occipital (PGO) waves spontaneously occur in the pons, lateral geniculate body (LGB), and occipital cortex during rapid eye movement sleep (REM), and PGO-like waves (PGO_E) may be elicited in LGB during sleep and waking. Because REM has been hypothesized to be a state of continual “orienting” or “hyper-alertness,” we tested whether the amplitudes of PGO_E in “alerting” situations (the abrupt onset of a loud sound or presentation of a novel stimulus within a series of stimuli) that evoke orienting responses (OR) would be greater than those following stimuli without OR. We also compared PGO_E accompanying OR to PGO_E during REM and NREM when OR are absent. The amplitudes of PGO_E in W were greatest when OR were observed, and the amplitudes of PGO_E accompanying OR were not significantly different from PGO_E amplitudes in REM. Likewise, the amplitudes of PGO_E during REM were not significantly different from those of the highest amplitude spontaneous PGO waves. We propose that the presence of PGO_E signals registration of stimuli and that stimuli of sufficient significance to induce behavioral OR in waking also elicit PGO_E of significantly greater amplitudes in all behavioral states. These findings support the hypothesis that the presence of high-amplitude PGO waves in REM indicates that the brain is in a state of more-or-less continual orienting.

Key words: Elicited PGO waves; Lateral geniculate body; Orienting; Sleep; Rapid eye movement sleep

Rapid eye movement sleep (REM) may be a paradoxical state of continual “orienting” (Morrison 1979). Several lines of evidence support this suggestion: activity in the central nervous system is much the same during REM as during alert wakefulness (e.g., low voltage, high frequency EEG; hippocampal theta) even though overt behavior is inhibited. Also, cats with pontine lesions that eliminate the atonia of REM spontaneously emit behaviors outwardly similar to orienting without apparent influence from the environment (e.g., Jouvet and Delorme 1965; Henley and Morrison 1974; Sastre and Jouvet 1979; Hendricks et al. 1982). A spontaneous phasic event of REM, the ponto-geniculo-occipital (PGO) wave, may be a central marker of the normally suppressed spontaneous “orienting” of REM. PGO waves normally occur spontaneously in the

pons, lateral geniculate body (LGB) and occipital cortex during REM (Jouvet 1967). An elicited analog of the PGO wave (PGO_E) may be obtained in sleep and waking by “alerting” stimuli that also elicit the behavioral orienting response (OR) in waking (Ball et al. 1991a, b; Sanford et al. 1992a, b).

We have studied the relationship of PGO_E to OR in waking, REM and non-REM (NREM) by examining rates of habituation to relatively intense tones (Ball et al. 1991b; Sanford et al. 1992a, b). We have found that PGO_E dissociate from OR in waking, continuing to be elicited long after OR habituate. During normal sleep OR were not present, of course; but PGO_E were obtained at higher amplitudes than in waking.

In the habituation studies we noticed, but did not specifically study or quantify, a tendency for elevated PGO_E amplitude on the initial presentation of a tone stimulus. These observations fit well with the observation that the highest amplitude waves in LGB occur when an animal responds to an unexpected stimulus (Bowker and Morrison 1976, 1977; Bowker 1984). However, Bowker and Morrison's (1976, 1977) early, but limited, behavioral study, which revealed that such stimuli (auditory, olfactory and visual) elicit high-am-

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plitude waves together with searching activity, has not received further attention, and no one has examined isolated PGO_E and OR responses to the abrupt onset of a stimulus or change in stimulus quality. It is well established that any change in stimuli presented in a series will re-elicite OR (e.g., Sokolov 1969). Determining the factors which elicit high-amplitude PGO_E in waking could yield valuable insights into the nature of REM, which has high-amplitude spontaneous PGO waves and PGO_E (e.g., Wu et al. 1989; Ball et al. 1991b).

The specific aims of the present work, then, were to determine if the amplitude of PGO_E related directly to OR in waking in response to auditory stimulus onset and to a novel stimulus presented in a series of stimuli, and whether the amplitudes of PGO_E within REM and NREM would compare to those in alerting situations during waking. To accomplish these aims the first responses in blocks of auditory stimuli separated by at least 20 min (stimulus onset) in waking were compared to responses obtained in REM and NREM; PGO_E within REM were compared to spontaneous PGO in REM; and responses to novel stimuli in waking were compared to responses to habituation stimuli. Two previous studies with similar designs (Ball et al. 1991b; Sanford et al. 1992b) provided data from which to determine the relationship of PGO_E and OR during stimulus onset. A subset of cats from these studies was presented with novel auditory stimuli in a separate experiment.

Methods and materials

The basic methods and materials have been described in detail previously (Ball et al. 1991b; Sanford et al. 1992b). Thirteen adult, female cats were implanted with standard electrodes for recording physiological sleep. Tripolar stainless-steel electrodes were implanted in LGB bilaterally for recording PGO waves and PGO_E (AP: +6.0; ML: +/−10; DV: +2.7; Berman 1968). Stereotaxic surgery was performed under sterile conditions using halothane anesthesia. Nalbuphine (2.5 mg/kg, s.c.) was administered to control potential post-operative pain.

PGO_E were defined as those waves recorded from LGB with post-stimulus latencies between 40 and 160 msec and having peak amplitudes of at least 30% that of the mean amplitude of the 10 highest elicited waves. Analyses of PGO_E were conducted on amplitude (mean peak voltage of responses excluding trials with no detectable response) and proportion (number of responses/number of stimuli) in each block. OR were scored from videotapes using a scale adapted from Ursin et al. (1969). OR scores were derived from pre- and post-stimulus differences in body posture and head

and ear movements (described in Ball et al. 1991b). Analyses for OR were conducted on difference scores (mean difference score excluding trials with no discernible OR) and proportion.

To examine the effect of stimulus onset, data were combined from 12 cats from previous experiments (Ball et al. 1991b; Sanford et al. 1992b) and one additional cat that experienced similar protocols. All cats were allowed at least 7 days to recover from surgery and were habituated to the recording chamber over 5 days of baseline sleep monitoring. The cats received a minimum of 5 blocks of at least 40 tones (90–100 dB SPL; 1000 or 4000 Hz sine wave; 90 msec duration; 5 msec rise time; 2 sec interstimulus interval) or white noise bursts (100 dB SPL; 20 Hz to 50 kHz; 90 msec duration; 5 msec rise time; 2 sec interstimulus interval) in waking, followed by tones presented throughout a sleep state (REM or NREM on separate days 1 week apart) and then a final block of tones in waking. The first 5 waking blocks were spaced 20 min apart and the last waking block occurred 20 min after testing in the sleep state. Testing in REM or NREM was counterbalanced across days and cats. For analyses, the first responses in each waking block were compared to responses in REM and NREM.

To examine the effect of novel stimuli, 8 awake cats were presented with 140, uninterrupted, 100 dB stimuli at 2 sec interstimulus intervals in either of the following 2 orders: (1) 80 tones (habituation), 20 white noise bursts (novel), plus 40 more tones (habituation), or (2) 80 white noise bursts (habituation), 20 tones (novel), and 40 more white noise bursts (habituation). Each cat received both orders of stimuli on 2 separate days 1 week apart. The orders of stimulus condition were counterbalanced across days to control for order effects. For analysis, the 140 trials were divided into 7 blocks of 20 trials each. Statistical analyses were conducted on the first response in each block of 20 stimuli, thereby allowing comparisons of responses to habituation stimuli to those to novel stimuli.

Two (Day or Stimulus condition) × 7 (Block) within-subjects analyses of variance (ANOVAs) were conducted except as noted. Post hoc tests were conducted with Tukey's HSD test with $P < 0.05$. Trials with movement artifacts or ambiguous responses were not considered in the analysis.

Results

Overview of results

PGO_E amplitudes in response to stimulus onset in waking closely approximated those of PGO_E in REM. High amplitude PGO_E in waking were closely associated with OR. PGO_E of relatively lower amplitudes continued to be elicited throughout the stimulus block

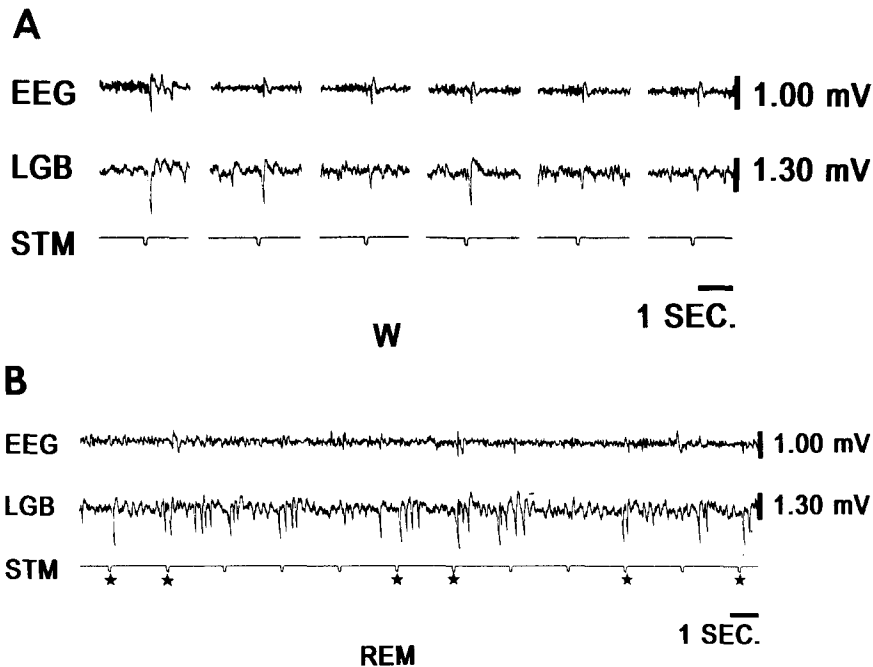


Fig. 1. A: excerpts from the polygraph record of one block of tones in wakefulness for cat L13 demonstrating relatively higher amplitude PGO_E to the first stimulus presentation. B: polygraph recordings showing PGO_E and spontaneous PGO in REM in cat L13. Stars indicate elicited waves in REM as determined by the latency criterion.

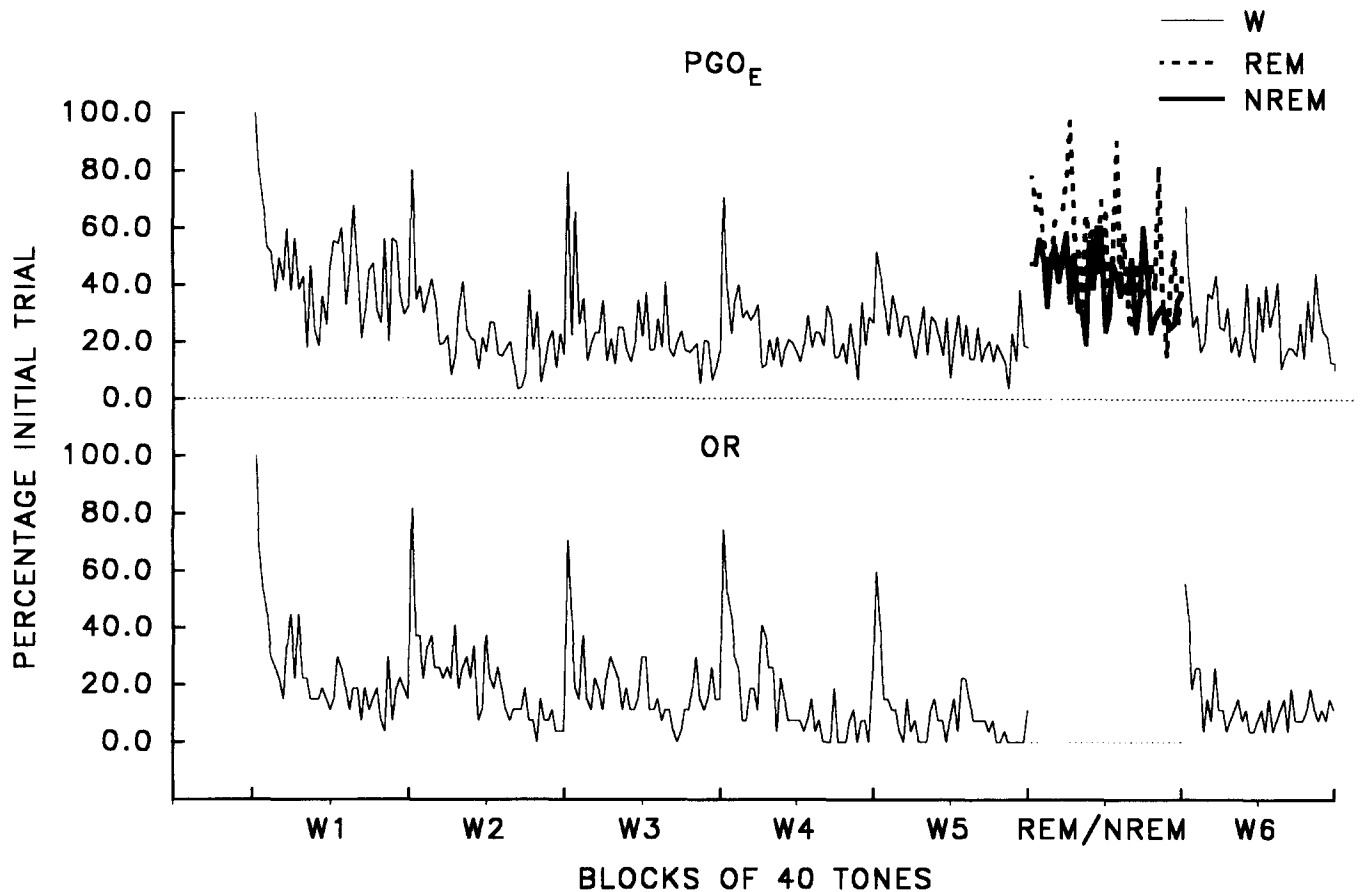


Fig. 2. OR and PGO_E across trials for each block in W and in NREM and REM considered as a percentage of the initial trial. Note that the W data came from day 1 of testing and the data for NREM or REM could have been collected on either day 1 or day 2 of testing. Relative change across trials is a reflection of proportion as well as amplitude and difference score. $N = 13$.

in waking, whereas OR habituated rapidly. The amplitudes of these PGO_E , which did not accompany noticeable OR, were significantly lower than the amplitudes of PGO_E in REM. The amplitudes of PGO_E in REM were not significantly less than those of the largest spontaneous PGO waves. PGO_E amplitudes in NREM were less than those in REM, and not significantly different from those in waking.

The initial tone or white noise stimulus (habituation stimuli were novel when first presented) elicited OR and high amplitude PGO_E . The presentation of a novel stimulus re-elicited OR which were accompanied in 5 of 8 cats by noticeable, yet non-significant, increases in PGO_E amplitude.

Initial PGO_E response in waking vs. PGO_E in sleep states

High-amplitude PGO_E occurred in response to stimulus onset in waking, whereas PGO_E in response to tones later in the block could have lesser amplitudes (Fig. 1A). The amplitudes of PGO_E in response to stimulus onset were not significantly lower than the amplitudes of PGO_E in REM (Figs. 1B and 2). Note in Fig. 1B that spontaneous PGO waves occur singly, as do PGO_E , as well as in bursts associated with rapid eye movements, which are not included in this figure (Morrison and Pompeiano 1966). In contrast, the mean amplitudes of PGO_E elicited in waking (based on the entire block) were significantly less than the amplitudes of those elicited during REM, $F(6, 72) = 6.14$, $P < 0.001$.

The amplitudes of PGO_E in NREM were not significantly different from those of either first response PGO_E or mean PGO_E (considering the entire block) in

waking. This was due to the amplitudes of PGO_E in NREM being intermediate (see Fig. 2) to the high amplitudes of first response PGO_E and the lower amplitudes of PGO_E obtained throughout the block.

High-amplitude PGO_E in waking were closely associated with OR (Fig. 2). Both PGO_E and OR occurred most often during stimulus onset in each waking block on each test day. OR did not occur in NREM or REM.

Elicited and spontaneous PGO during REM with stimulus presentation

The amplitudes of PGO_E elicited during REM were compared to the amplitudes of PGO waves spontaneously occurring across the REM episode. Because we could not rule out the possibility that tones could influence the amplitudes of PGO waves occurring outside our accepted response latencies, we compared PGO_E to PGO waves occurring at two different post-stimulus latencies. PGO waves were extracted from the data record during two 120 msec time windows, the length of window we use for PGO_E (PGO_E : 40–160 msec; PGO_1 : 200–320 msec; PGO_2 : 1880–2000 msec). Additionally, the highest amplitude PGO wave occurring in the interstimulus interval was extracted (PGO_3 : 200–2000 msec).

Fig. 3 illustrates in graph form the comparisons among these 4 measures. For analysis, we divided the REM episodes into quartiles (by time). The data were analyzed with a 4 (PGO extraction) \times 4 (quartile) ANOVA with repeated measures on both factors. There was a significant effect for PGO extraction, $F(3, 36) = 11.12$, $P < 0.001$, indicating differences in wave amplitudes among the 4 extractions. Therefore, we compared the amplitudes of PGO_E to those of each of

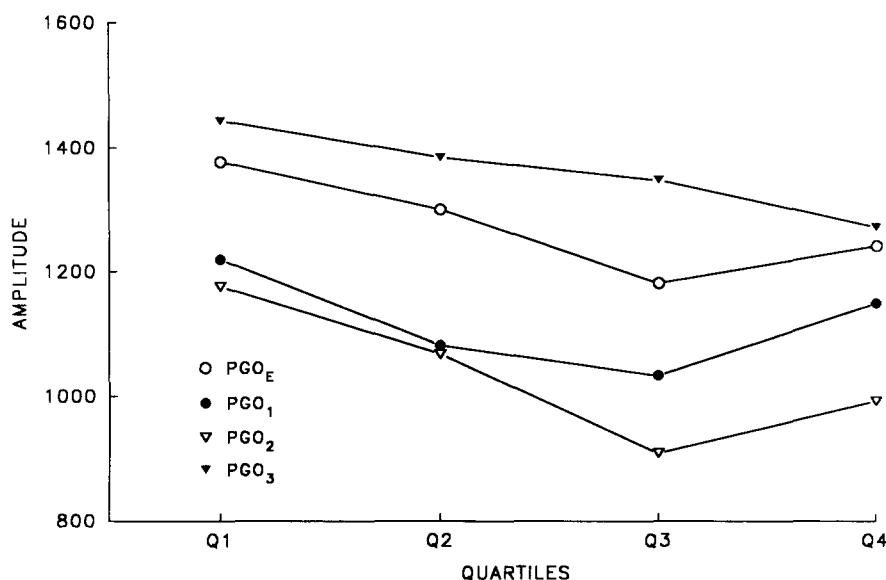


Fig. 3. PGO_E and spontaneous PGO waves across quartiles during REM. PGO_E : from 120 msec bin post stimulus. PGO_1 : 120 msec bin between 200 and 320 msec post stimulus. PGO_2 : 120 msec bin immediately prior to stimulus onset (1880–2000 msec post stimulus). PGO_3 : largest PGO wave in interstimulus interval (from 200 to 2000 msec).

the spontaneous extractions. The amplitudes of PGO_E were greater than those of PGO_1 , $F(1, 12) = 7.84$, $P < 0.016$, and PGO_2 , $F(1, 12) = 17.55$, $P < 0.001$, and were not significantly different from those of the highest amplitude PGO_3 waves ($P < 0.151$) (Fig. 3).

During REM there is the possibility that a spontaneous PGO wave may be accepted as an elicited wave. In order to determine how often this occurs, and to correct our estimate of how often PGO_E are actually elicited during REM, we examined the number of waves occurring during the extraction windows for PGO_E , PGO_1 and PGO_2 . The proportion of trials with PGO_E was higher than that of PGO_1 , $F(1, 12) = 24.53$, $P < 0.001$, and PGO_2 , $F(1, 12) = 23.83$, $P < 0.001$, affirming that PGO_E were responses to stimuli. We were able to determine that PGO_E are elicited on 30–40% of stimulus presentations. There were no significant differences between PGO_1 and PGO_2 , or between blocks for any extraction, including PGO_E .

Effect of novel stimulus

Fig. 4 illustrates the effects on PGO_E amplitudes and OR difference scores of 140 stimuli at 2 sec intervals: 80 tones or white noise followed by 20 different stimuli and then a return to the original stimulus. Each point represents the initial response in each of 7 blocks of 20 stimuli. PGO_E of noticeably greater amplitudes were recorded on the first trial in block 1 and on the first novel stimulus trial compared to the first response in the other blocks. Our intent was to examine responses on day 1 of testing when neither stimulus had been experienced and compare those with responses on day 2 of testing when both stimuli were no longer truly novel. However, a significant interaction, F

$(6, 30) = 2.67$, $P < 0.034$, suggested that tones and white noise bursts may have had differential effects on PGO_E amplitude which would have clouded the interpretation of the planned analysis. The interaction resulted from the amplitudes of the first PGO_E in response to white noise in block 1 being significantly greater than the first responses in succeeding blocks, including those to novel stimuli (Tukey, $P < 0.05$).

OR occurred most often in response to the first stimulus in block 1 and to novel stimuli than to habituation stimuli in other blocks, $F(6, 42) = 14.51$, $P < 0.001$. This would seem to suggest a dissociation between the mechanisms of OR and PGO_E . However, the qualitative nature of our measure of behavioral OR did not allow us to determine unequivocally whether OR was differentially affected by tone or white noise. There was no significant effect for day of testing.

Discussion

The results suggest that the amplitude of PGO_E can signify more than the mere sensory registration of a stimulus. The abrupt onset of a stimulus in waking, even one that has been presented many times, simultaneously elicits high-amplitude PGO_E and OR, though PGO_E with lesser amplitudes may continue to be elicited in the absence of observable OR on further presentations of the stimulus. Furthermore, the abrupt onset of a stimulus appears to reintegrate PGO_E and OR with as little as a 20 min pause in stimulus presentations. This suggests that neurons (we predict in the reticular formation) identify a signal that requires attention and that this requirement is passed via peri-

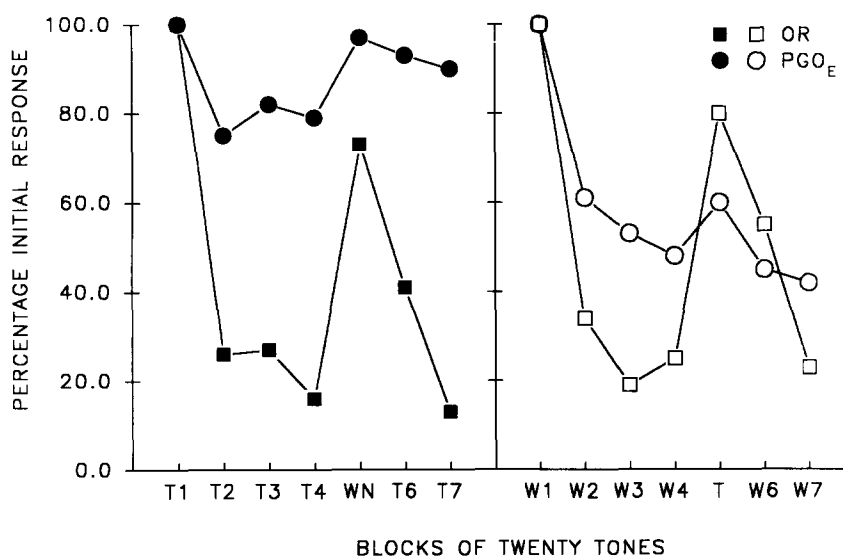


Fig. 4. The amplitude of the first PGO_E and first OR difference score in each of 7 blocks of 20 trials plotted across blocks in conditions of tones, white noise, tones or white noise, tones, white noise. Unlike the experiment represented by Fig. 2, the stimuli were presented continuously at 2 sec intervals. The data have been transformed as a percentage of the initial response in block 1 in order to plot OR on the same axis as PGO_E . Note the relatively higher amplitudes of PGO_E which accompanied OR elicited by the first stimulus presentation and by the presentation of a novel stimulus. Relatively higher PGO_E were observed in 5 of the 8 cats tested. W: white noise. T: tone.

brachial neurons in the dorsal pons that respond to auditory stimuli and also generate PGO waves (Steriade et al. 1990). Thus, PGO_E in LGB could reflect a honing of neural mechanisms in the visual system to receive information (Bowker and Morrison 1977; Singer 1973, 1977).

The recovery of OR in response to novel stimuli was accompanied by noticeably larger PGO_E amplitudes in 5 cats. It should be mentioned that the remaining 3 cats were sluggish and in general showed little response to auditory stimuli of the intensities we used. The positive results in 5 cats strongly suggest that the amplitudes of PGO_E may be increased by novel stimuli as well as by stimulus onset. However, due to the significant interaction between tone and white noise habituation stimuli, we cannot unequivocally conclude that the effects were due to the novelty of the stimulus. Instead, our results indicate that white noise bursts of the intensity and duration that we used may actually be somewhat more effective than tone for eliciting high amplitude PGO_E. Even so, these results suggest that the amplitudes of PGO_E are greater in situations that elicit OR. Unfortunately, our behavioral measure was a limited indicator of OR magnitude and we were unable to determine whether relatively greater overt OR occurred in response to white noise. It has been demonstrated, though, that any change in stimulus parameters will re- elicit OR after habituation (Sokolov 1969). Thus, in retrospect, a more appropriate test would have been to change parameters of the tone burst (e.g., intensity or frequency), which would have introduced novelty without producing the dramatic contrast in stimulus efficacy evident between white noise and tone.

Because high-amplitude PGO waves occur spontaneously in REM and PGO_E of similar high amplitudes accompany OR in waking, we suggest that the spontaneous PGO waves of REM may mark the endogenous activation of mechanisms underlying OR that typically are triggered by stimuli in waking. That spontaneous PGO waves in REM may be most closely related to orienting is further supported by the observation of orienting-like behaviors in cats during REM without atonia episodes (Jouvet and Delorme 1965; Henley and Morrison 1974; Sastre and Jouvet 1979; Hendricks et al. 1982; Soh et al. 1992). Cats in this state are capable of various behaviors ranging from lifting their heads to locomotion. Certain cats exhibit "fly-watching" in which they appear to be attending to a visual stimulus in the environment when there is none.

Recently, we demonstrated externally elicited OR during REM without atonia in two cats capable of locomotion in REM-A. These cats turned their heads toward speakers producing tone stimuli of varying intensities (Morrison et al. 1991). A third cat capable of spontaneous head raising exhibited ear-pinna rotation

but no head turning in response to tones. Head orienting and ear-pinna rotation may be distinguished from head startle and ear flicks, indicating that the mechanisms underlying these responses involve attentional processes. Three cats with less release of muscle tone, two capable of righting with their forequarters, did not exhibit orienting to external stimuli. Thus, a mere increase of muscle tone is insufficient to release OR in REM without atonia and is not enough to insure head OR. This suggests that the inhibition of overt OR during sleep is not due solely to a loss of muscle tone, but instead may involve an inhibition of neural mechanisms that initiate behavioral OR. The mechanisms which allow central registration of stimuli in REM without arousal and overt responding are unknown since atonia does not appear to be the only factor involved.

High-amplitude PGO_E appear to be indicators of external activation of central components of OR in all states, and high-amplitude spontaneously occurring PGO waves may well indicate endogenous activation of those components during REM. The parallel plots across quartiles in REM for PGO_E, PGO₁ and PGO₂ (Fig. 3) suggest that the same neural mechanisms may underlie both spontaneously occurring and elicited PGO waves. This suggestion is bolstered by the finding that the amplitudes of PGO_E are linked to those of temporally close PGO waves in REM (Wu et al. 1989). Also, neurons in the peribrachial area of the pedunculo-pontine tegmentum that fire in bursts prior to spontaneously occurring PGO waves (McCarley et al. 1978; Sakai and Jouvet 1980; Nelson et al. 1983) may be activated by "handclaps" although an accompanying PGO_E may not always be recorded (Steriade et al. 1990).

A potential limitation of this work is that we were unable to determine the direction of eye movements during OR with our methodology. Eye movements are closely associated with PGO waves in REM (e.g., Brooks 1968; Brooks and Gershon 1971; Nelson et al. 1983) although they are absent during the transition period when PGO waves have the highest amplitudes prior to true REM. In waking, spontaneously occurring waves recorded from LGB and accompanying eye movements have typically been called eye movement potentials to distinguish them from the PGO waves of REM (e.g., Brooks 1968; Brooks and Gershon 1971). Eye movements also may accompany PGO_E (e.g., Bowker and Morrison 1977). However, there is a close coupling between head and eye motor systems in cats (e.g., Guitton et al. 1990) suggesting that behavioral observations of head movements should give results similar to those found with recordings of eye movement direction.

Nelson et al. (1983) found that, in REM, PGO wave amplitude was greater in LGB ipsilateral to the direc-

tion of rapid eye movement compared to that in the contralateral LGB. In contrast, Cespuglio et al. (1976) drew opposite conclusions in a study using different methodology: macropotentials recorded from the abducens nucleus, and accompanying inhibition of the lateral rectus, were associated with larger PGO waves in the ipsilateral LGB. No one has studied eye movement direction and PGO_E. It is known that the temporal relationship of eye movement and PGO_E may vary with stimulus modality; auditory and olfactory elicited PGO_E precede eye movement, whereas visually elicited PGO_E follow eye movement (Bowker and Morrison 1977). It is also known that the amplitudes of eye movement potentials in LGB are approximately 50% of those of PGO waves in REM (e.g., Brooks and Gershon 1971) and that the amplitudes of PGO_E in waking in response to habituation stimuli are significantly less than those of PGO_E in REM (e.g., Ball et al. 1991b; Sanford et al. 1991b). Our data indicate that the amplitudes of PGO_E in response to stimulus onset, and perhaps novel stimuli as we presented them in waking approximate those of PGO_E in REM. This finding, along with evidence in the literature, suggests two very important questions that need to be addressed in order to understand more fully the relationship between PGO_E and OR: do stimulus onset and novel stimuli increase PGO_E amplitude bilaterally, and is there a relative increase in one LGB which is correlated with eye movement directionality?

The present work refines our view of PGO_E as an indicator of brain alerting. We propose that the mere presence of PGO_E indicates that stimulus information has been registered, and that brain alerting mechanisms have been readied, though an overt behavioral response may not be forthcoming. Specific stimulus qualities (e.g., stimulus onset, and probably novel stimuli as well), integrate central and peripheral response mechanisms such that overt action is taken. Activation of central orienting mechanisms is reflected in larger amplitude PGO_E. The presence of high-amplitude PGO_E accompanying OR in waking, the high-amplitude PGO waves of REM and the spontaneous "OR" of REM without atonia, support the idea that certain brain orienting mechanisms are spontaneously activated during REM (Morrison 1979; Morrison and Reiner 1985). Indeed, the brain in REM and alert wakefulness is functioning in essentially similar ways (Morrison 1979; Llinás and Paré 1991).

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