Alerting effects on choice reaction time and the photic eyeblink reflex

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Abstract

To test the possibility that a common mechanism might be responsible for alerting effects on voluntary and reflexive reactions, choice reaction times (RT) to intense flashes of light were compared with eyeblink reflexes simultaneously evoked by those stimuli. An acoustic accessory stimulus, irrelevant to the RT task, facilitated both voluntary and reflexive reactions. A time uncertainty manipulation also generated facilitation of both responses under conditions in which phasic arousal was presumably greatest. However, there were several dissociations between alerting effects on voluntary and reflexive reactions and between effects on the early and late subcomponents of the photic orbicularis oculi reflex. In conjunction with other research in humans and animals, these data support the assumption that alerting involves the activation of multiple neuromodulatory (e.g., monoamine) systems, each of which is characterized by a distinct behavioral, neuropharmacological, and electrophysiological profile.

Keywords: Attention; Audition; Brain-stem reflex; Foreperiod; Startle blink; Vision

1. Introduction

Presentation of a nonreflexogenic prepulse at approximately the same time as a reflex eliciting stimulus has been found to produce facilitation relative to no-prepulse control trials (reviewed in Brunia et al., 1985; Hackley and Boelhouwer, 1996). The onset asynchronies at which this facilitation is manifested vary across diverse stimuli and responses. For example, an airpuff to the neck facilitates the knee-jerk reflex at lead times of 100–600 ms (Bowditch and Warren, 1890). In contrast, for potentiation of the eyeblink response to supraorbital nerve stimulation (R2 component) by an acoustic prepulse the effective stimulus onset asynchronies extend from +10 to −60 ms (e.g. Boelhouwer et al., 1991; negative asynchronies indicate that the prepulse follows the reflexogenic stimulus).

In parallel with these findings from reflex physiology, psychologists have shown that a task-irrelevant accessory stimulus delivered at about the same time (e.g. asynchronies of +112 to −35 ms; Bernstein et al., 1970) as a reaction stimulus reliably speeds choice reaction time (RT). In such experiments, the accessory is irrelevant in the sense that it does not provide information either about which response the subject should select or about when the reaction stimulus will be delivered (e.g. Schmidt et al., 1984; reviewed in Nickerson, 1973). If the prestimulus is presented in advance of the reaction stimulus and if it does predict when that stimulus will occur, it is instead conventionally referred to as a warning signal. Warning and accessory effects on RT are apparently related, because these facilitatory effects interact (e.g. Stoffels et al., 1985) and they are both often accompanied by an increase in error rate (e.g. Posner et al., 1973).

Research concerning prestimulus facilitation of voluntary and reflexive reactions has been pursued more or less independently for over a century (e.g. Bowditch and Warren, 1890; Wundt, 1880, cited in James, 1890). However, a parallel study of these two response categories by Zeigler (1982) constitutes a notable exception. In that unpublished study, warning signals were demonstrated to simultaneously facilitate the latency of eyeblink reflexes and instructed keypress responses to intense stimuli. The facilitation was reliable across acoustic, visual, and tactile warning and reaction stimuli (+2000 ms onset asyn-
chrony). Such findings support the working hypothesis that there is an approachable degree of overlap in the mechanisms underlying prestimulus effects on voluntary and reflexive reactions (cf. Graham, 1975; Keuss and van der Molen, 1982).

Both within psychology (Posner, 1978; Sanders, 1980) and physiology (Graham; 1975; Robbins and Everitt, 1995), the most prominent theories of prestimulus facilitation all assume that the underlying mechanisms involve alerting (or immediate arousal, as it is also known). The principal controversy in the RT literature concerns which information processing stage or stages are influenced by alerting. On the one hand, Sanders (1980, 1983) has argued that alerting facilitates a low level motor process. In support of this assumption, the effect of tonic muscle tension on RT has been found to interact with accessory presence/absence but not with perceptual or decision factors (e.g. Sanders, 1980; cf. Schmidt et al., 1984). Posner (1978, pp. 130–131), on the other hand, has hypothesized that alerting influences a central, decision-level mechanism. This theory can account for the increased error rate that frequently accompanies phasic alerting. According to this interpretation, sensory evidence regarding the identity of a choice-RT stimulus builds up at a constant rate. The central mechanism responds more quickly, but on the basis of less evidence, given the transient increase in arousal triggered by a warning or an accessory stimulus. Thus, voluntary responses are speeded, but the reduction in RT may be compromised by an increase in errors.

In the reflexology literature, there is little controversy about the general locus of alerting effects. All studies to date indicate that such phenomena involve modulation of low level motor processes (e.g. acoustic startle in rats (Davis et al., 1982), masticatory H-reflex in cats (Stafford and Jacobs, 1990), nictitating membrane component of the eyelid reflex in rabbits (Young et al., 1976)). If it could be shown that a common mechanism underlies alerting effects on voluntary and reflexive responses this would support Sanders’ (e.g. 1980) theory that warning and accessory effects on RT involve the modulation of motoric processes. Because reflexes do not involve a decision stage at which stimuli can be arbitrarily mapped onto responses, evidence for a common mechanism would argue against Posner’s (e.g. 1978) hypothesis of a decision-level locus for alerting effects.

With this in mind, we attempted to directly compare the alerting effects of accessory and warning stimuli on voluntary and reflexive reactions. Human subjects made speeded choice reactions to bright flashes of light while the photic eyelid reflexes evoked by these stimuli were recorded. Our rationale was that similarities in the pattern of results for voluntary and reflexive reactions would support the common mechanism hypothesis, whereas dissimilarities would argue for a divergence in underlying mechanisms.

2. Materials and methods

2.1. Subjects

Thirty-one introductory psychology students at the University of Missouri-Columbia received extra credit for participation in this experiment. Of these 31 subjects, 11 were omitted from the final data analysis (5 for experimenter error or equipment failure; 3 because of blinking to the accessory stimulus; 1 for lack of measurable blink; 1 due to excessively slow reaction times; and 1 for failure to follow instructions). The remaining 20 subjects ranged in age from 18 to 31 years, with a median age of 19. All except 3 were right handed according to self-report, 12 were female. Nine subjects normally wore corrective lenses, but they removed them prior to the experiment. All subjects gave their informed consent prior to participation.

2.2. Apparatus

Subjects were seated at a table upon which was mounted a clinical perimeter with chin and forehead rest (American Optical Co., model 480). Two 22° (14 cm) wide strobe lamps were mounted on the perimeter at a distance of about 32 cm from the subject’s face. The lamps were positioned at symmetrical locations, centered 18° to the left and right of a red, 0.8° wide, light-emitting diode (LED) that served as fixation point and warning signal. To reduce light scatter, the strobes were equipped with 5 cm louvres made of black construction paper. The strobes were individually controlled by Grass Instrument Company driver units, model PS-22. The intensity of the 2 ms flashes was set to '1' which, according to the manufacturer’s specification, corresponds to approximately 1.5 millilumen-seconds/cm² at a distance of 25 cm. Continuous white noise, 55 dB (SPL), was delivered binurally over Telephonics TDH-50P headphones to mask the click produced during lamp discharge. The accessory stimulus had an intensity of 80 dB, a rise/fall time of 40 ms, a plateau of 150 ms, and an onset 40 ms prior to that of the strobe. Isometric grips were mounted under the strobe lamps on the right and left sides of the table. Presentation of the experimental stimuli and data acquisition were controlled by an Intel 286-based computer located in an adjacent room.

2.3. Procedure

Subjects were told to fixate on the central diode when it appeared and to squeeze the grip located on the side of the strobe flash. Both speed and accuracy were emphasized. They were also told that they would often hear a tone pip at about the same time as a light flash, but that this was irrelevant to the task and could be ignored.

After a 16-trial practice block, the electrodes were
applied. An occlusive eyepatch was placed over the recorded eye (left for half of the subjects) to minimize contamination of the EMG by evoked retinal potentials (Hackley and Johnson, 1996). The convex plastic eyepatch did not press against the eye itself, so subjects could blink freely. Prior to the start of the experiment, subjects were given 10 min for adaptation to the near-scotopic room illumination.

The experimental session consisted of 8 blocks of 30 trials, each of which began with the onset of the red fixation light which persisted through the recording epoch. After a randomly chosen foreperiod of 1500 or 4000 ms (hereafter referred to as ‘short’ and ‘long’), subjects were presented with 1 of 3 events: A reflex-eliciting strobe flash on the right or left of fixation accompanied by a binaural accessory tone; a right or left strobe flash alone; or a binaural accessory tone alone. Thus, there were 8 conditions requiring a response (accessory present/absent × foreperiod long/short × strobe left/right) and two accessory-alone catch trial conditions (short/long foreperiod) that required the subject to withhold the response. The 10 conditions occurred randomly with equal probability within each trial block. The intertrial interval varied randomly from 6 to 10 s, well beyond the relative refractory period for the photic blink reflex (Zwaardemaker and Lans, 1899, cited in Dodge, 1913). The interblock interval was 1–2 min with the exception of a 5 min break after the fourth block.

2.4. Recording

Electrophysiological activity was recorded using Ag-AgCl surface electrodes and Grass EC-2 paste. Reflexive EMG bursts were recorded from the orbicularis oculi muscle with two electrodes centered below the pupil on the lower lid. Horizontal electrooculograms (H-EOGs) were recorded with electrodes positioned about 2 cm lateral to the outer canthus of each eye. The two electrodes on each arm were placed over the flexor digitorum profundus muscle, at positions that traversed the distance from the elbow to the wrist (see Lipold, 1967). The bandpass for the Grass Model 12 amplifiers was 30–300 Hz for eyelid and forearm EMG and 0.01–100 Hz for H-EOG. (These filter cutoffs represent 6 dB attenuation points, with a 12 dB/octave rolloff for the high pass filter and a 6 dB/octave slope for the low pass filter.) Care was taken to avoid excessive abrasion of the skin, but electrode impedances were always less than 12 kΩ. Analog-to-digital conversion was carried out at a rate of 1000 Hz, with the recording epoch beginning 30 ms prior to strobe onset and lasting a total of 512 ms.

2.5. Data analysis

Blink EMG was full wave rectified and then signal averaged according to trial condition, with averaging time-locked to strobe onset. Trials with excessive EMG activity during the baseline period (e.g. spontaneous, non-reflexive blinking) or suspected shifts in gaze prior to blink onset, and those with incorrect voluntary responses were excluded from the averages (5.6 and 5.8% of total trials, respectively). Averaged waveforms were digitally smoothed with 3 passes of a 3-point boxcar filter. Computer measurement of reflex mean amplitude was calculated for each trial type within a window of 50–80 ms for R50 and 90–200 ms for R80. Poor signal-to-noise ratios for blink EMG precluded measurement of latencies on individual trials. Consequently, the fractional (50%) peak latency of R50 was measured within a time window of 50–80 ms. To obtain this value, the computer first searched for the highest peak within the window and then proceeded backward to the first point in time at which 50% of that peak was reached. Mean amplitudes of forearm EMG were measured within a window of 150–350 ms. Latency of forearm EMG, however, was measured by a computer program for each individual trial. Preliminary analyses indicated that single trial means were more sensitive than measurements on the signal-averaged waveforms and, in addition, this type of analysis conforms more closely to that of the traditional RT literature.

Per condition means were subjected to 2(patch right/left) × 2(accessory present/absent) × 2(foreperiod short/long) × 2(strobe left/right) mixed analyses of variance with eyepatch location as a between-groups factor. In addition, 2 correlational analyses were performed. First, a Pearson correlation coefficient was computed to assess the relationship across subjects between the facilitation effects of an accessory on forearm EMG versus blink reflex EMG. The effect of the accessory on R50 and on forearm EMG was determined by calculating a percent change score such that a positive number indicated facilitation under the accessory present conditions (collapsing across all other factors) for both latency and magnitude. A similar analysis evaluated the relationship between facilitation of voluntary and reflexive EMG responses after a variable foreperiod. The effect of foreperiod on forearm EMG and on the R50 blink component were determined for each subject by calculating a percent change score such that a positive number indicated facilitation under the long, relative to the short, foreperiod conditions (collapsing across all other factors) for both latency and magnitude. The reliability of all effects was tested at the $P < 0.05$ level.

3. Results

3.1. Error analysis

The correct response was made on 92.6% of the total trials. Subjects failed to make a response within the measured time window on 2.5% of the trials and re-
sponded incorrectly (i.e. with the wrong hand or with both hands) on 4.8% of the trials. Anticipations were defined as any forearm response with an onset latency less than 100 ms; these errors were rare (0.1% of trials summed across all subjects).

To investigate the possibility of a trade-off of accuracy for speed, a repeated measures analysis of variance was performed on trials with mistakes of any kind (two hand, wrong hand, or anticipations). Consistent with prior research (e.g. Posner et al., 1973), more errors were made on trials in which the accessory was present compared to trials in which the accessory was absent ($M = 5.9$ and 3.8%, respectively; $F(1, 18) = 5.3$, $P < 0.05$). However, foreperiod duration did not influence mistakes ($F(1, 18) < 1$). The error analysis also revealed a patch location by strobe location interaction, such that reactions to nasal hemifield stimuli (i.e. those activating ganglion cells whose axons do not cross at the optic chiasm) were less accurate than reactions to temporal hemifield stimuli ($F(1, 18) = 8.9$, $P < 0.01$; $M = 5.9$ and 3.9% errors, respectively). As shown by a 3-way patch × strobe × foreperiod interaction ($F(1, 18) = 14.6$, $P < 0.001$), this effect was stronger at short foreperiods ($F(1, 18) = 27.1$, $P < 0.001$) and was not reliable at long foreperiods ($F(1, 18) < 1$). All subsequently described analyses are based only on trials with a correct response.

3.2. Forearm EMG

The signal averaged waveforms for forearm EMG shown in Figs. 1 and 2 indicate a minimum onset latency of around 150 ms with a peak amplitude of approximately 75 μV (see Fig. 1). The latency analysis showed a reliable effect of accessory presence, with latency facilitated on trials which included a tone pip ($F(1, 18) = 69.8$, $P < 0.001$). Mean amplitude was also enhanced when the accessory accompanied the strobe, apparently reflecting a shift of EMG activity into the measurement window rather than an augmentation of force ($F(1, 18) = 18.3$, $P < 0.001$, Fig. 1).

Since the short and long foreperiods were presented randomly, we expected faster latencies at the long foreperiod due to the decrease in temporal uncertainty as the foreperiod aged: Just after detection of the warning signal, the subject should expect strobe presentation at 1.5 s with a probability of 40%. However, if the 1.5 s interval passed with no reaction stimulus, the conditional probability of strobe occurrence at 4.0 s would increase to 80%. Although both latency and amplitude did show a trend towards facilitation after a 4.0 s foreperiod as expected (Fig. 2), these effects failed to reach significance when the data were collapsed across accessory conditions ($F(1, 18) = 2.6$ and $F(1, 18) < 1$, respectively). However, when trials with and without an accessory were analyzed separately, the foreperiod effect on latency was quite reliable on the no-accessory control trials ($F(1, 18) = 9.9$, $P < 0.005$). This variation was reflected in an interaction of foreperiod duration with accessory presence, as shown in Fig. 3 ($F(1, 18) = 12.9$, $P < 0.002$). A similar interaction was found for mean amplitude ($F(1, 18) = 5.3$, $P < 0.05$, see Fig. 4), and the amount of amplitude facilitation by foreperiod was positively correlated across subjects with the amount of latency facilitation ($r(19) = 0.69$, $P < 0.001$).

Accessory presence also interacted with the location of the strobe, which was necessarily confounded with the hand of response in our design ($F(1, 18) = 12.2$, $P < 0.005$). Reactions were faster with the left hand when the accessory was absent, but there was little difference between right and left hands when the accessory was present. Alternatively, it could be said that the accessory had a greater effect on right hand than on the left hand responses.
Table 1
Means (SD) for forearm EMG latency (ms) and amplitude (μV)

<table>
<thead>
<tr>
<th>Stimulated eye</th>
<th>Accessory present</th>
<th>Accessory absent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FP short</td>
<td>FP long</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Left strobe</td>
<td>Right strobe</td>
</tr>
<tr>
<td>Latency</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left eye</td>
<td>259 (27)</td>
<td>268 (31)</td>
</tr>
<tr>
<td>Right eye</td>
<td>277 (35)</td>
<td>277 (34)</td>
</tr>
<tr>
<td>Amplitude</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left eye</td>
<td>41 (23)</td>
<td>39 (36)</td>
</tr>
<tr>
<td>Right eye</td>
<td>26 (22)</td>
<td>27 (27)</td>
</tr>
</tbody>
</table>

3.3. Blink reflex EMG

The two principal components of the photic blink reflex can be clearly seen in the grand average EMG waveforms of Figs. 1 and 2 (see also Table 2). The early component, labeled R50, has an onset latency of approximately 50 ms with peak latency between 60 and 70 ms, while the longer latency burst, R80, peaks at 130–140 ms.

![R50 Component](image1)

![Forearm EMG](image2)

The main effects for R50 were similar to those for forearm EMG (see Figs. 1 and 2, Table 2). Both R50 mean amplitude and R50 fractional peak latency were facilitated under conditions in which the accessory was present ($F(1, 18) = 13.7$, $P < 0.002$ and $F(1, 18) = 5.7$, $P < 0.05$, respectively). In addition, the long foreperiod produced facilitation relative to the short foreperiod, with this difference being significant for both latency and amplitude ($F(1, 18) = 11.6$, $P < 0.005$, and $F(1, 18) = 9.7$, $P < 0.01$, respectively). Unlike forearm EMG, however, accessory presence did not interact with foreperiod duration for any of the blink measures (all $F(1, 18) < 1$).

![R50 Component](image3)

![Mean Amplitude](image4)

![Mean Amplitude](image5)

Fig. 3. Fractional peak latency of R50 (top) and forearm EMG latency (bottom) as a function of foreperiod duration. Solid lines represent trials in which an accessory was present while dashed lines represent trials on which no accessory occurred.

Fig. 4. Mean amplitude for R50 (top) and forearm EMG (bottom) as a function of foreperiod duration. Solid lines represent trials on which an accessory was present while dashed lines represent trials in which no accessory occurred.
### Table 2
Means (SD) for reflex EMG fractional peak latency (ms) and mean amplitude (µV)

<table>
<thead>
<tr>
<th>Stimulated eye</th>
<th>Accessory present</th>
<th>Accessory absent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FP short</td>
<td>FP long</td>
</tr>
<tr>
<td></td>
<td>Left strobe</td>
<td>Right strobe</td>
</tr>
<tr>
<td><strong>R50 latency</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left eye</td>
<td>59 (5)</td>
<td>59 (4)</td>
</tr>
<tr>
<td>Right eye</td>
<td>61 (9)</td>
<td>63 (8)</td>
</tr>
<tr>
<td><strong>R50 amplitude</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left eye</td>
<td>6 (7)</td>
<td>6 (7)</td>
</tr>
<tr>
<td>Right eye</td>
<td>3 (3)</td>
<td>4 (4)</td>
</tr>
<tr>
<td><strong>R80 amplitude</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left eye</td>
<td>3 (2)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>Right eye</td>
<td>4 (3)</td>
<td>4 (3)</td>
</tr>
</tbody>
</table>

Analyses of R80 mean amplitude revealed accessory and foreperiod effects in the direction opposite to those observed for R50. Presentation of the accessory stimulus decreased R80 mean amplitude relative to responses on the no-accessory control trials (F(1,18) = 12.6, P < 0.002). Also, R80 was relatively inhibited on long compared to short foreperiod trials (F(1,18) = 7.4, P < 0.02). Thus, the R50 component showed a pattern of facilitation for the main effects of accessory and foreperiod similar to that found for forearm EMG, whereas R80 showed the reverse pattern. (Note reciprocal modulation has also been observed for the early and late components of the trigeminal blink reflex, e.g. Sanes and Ison, 1979).

Of additional interest was a trend in the data concerning activation of the blink reflex by crossed versus uncrossed ascending visual pathways. Specifically, a strobe location by patch location interaction approached significance for the mean amplitude of R80 (F(1,18) = 3.8, P < 0.07). Consistent with prior research at this lab (e.g. Hackley and Johnson, 1996), a flash in the temporal hemifield tended to evoke larger blinks than a flash delivered from within the nasal hemifield. These findings, as well as the nasal temporal asymmetry for error rates noted above, probably reflect the greater density of ganglion cells that cross at the optic chiasm. Because this anatomical difference is now known to exist for retinotectal as well as geniculostriate pathways (Williams et al., 1995), nasal temporal asymmetries are unlikely to represent a marker for extrageniculate visual functions, as has been proposed by Rafal and colleagues (e.g. Rafal et al., 1990).

#### 3.4. Correlational analysis

Because the effects of an accessory and, to a lesser extent, of foreperiod were similar for the voluntary EMG and the R50 EMG component of the blink reflex, a Pearson correlational analysis was used to investigate the degree of association across subjects. Facilitation of forearm latency by the accessory stimulus was not significantly correlated with R50 latency facilitation (r(19) = -0.34, P < 0.34), nor was forearm mean amplitude facilitation reliably correlated with R50 mean amplitude facilitation (r(19) = -0.06, P < 0.78). A similar analysis for warning interval effects also failed to document a reliable association between the modulation of voluntary and reflexive reactions (latency facilitation: r(19) = -0.32, P < 0.16; mean amplitude facilitation: r(19) = 0.13, P < 0.56). Although our sample size was modest, these null effects appear to constitute further evidence against any simple explanation of phasic alerting effects in terms of a single mechanism.

#### 4. Discussion

In this experiment, we used two manipulations that are commonly assumed to alter the level of phasic alerting. Our accessory and foreperiod manipulations yielded main effects and interactions for voluntary EMG responses that were quite similar to those previously reported for overt reaction time (e.g. Bernstein et al., 1970; Sanders, 1980). In addition, the facilitatory effect of the accessory stimulus on voluntary response latency was offset by an increase in error rate, a finding that is also common to many previous studies in the reaction time literature (e.g. Posner et al., 1973). In parallel with these findings, recordings of reflex EMG activity revealed facilitation of latency and amplitude in the accessory present and long foreperiod conditions.

Having obtained alerting effects on both voluntary and reflexive reactions within a single experiment, we are in a good position to make comparisons across these fundamental categories of motor activity.

Several notable dissociations were observed. First, the facilitating effect of an accessory on R50 latency and
amplitude was not correlated across subjects with facilitation of forearm EMG. Given prior research with pre-pulse facilitation of other reflexes (Young et al., 1976; Stafford and Jacobs, 1990; Boelhouwer et al., 1991), it appears likely that an accessory acts upon the motor pathway to speed the photic blink response. Thus, if a voluntary response were similarly modulated by an accessory acting upon low level motor pathways, as might be assumed under Sanders’ (1980) model, a positive correlation between accessory effects on reflexive and voluntary reaction would have been expected. This was not the case.

Second, with respect to the facilitation found after long relative to the short foreperiods, again no correlation was found between reflexive blink (R50) and forearm EMG for either magnitude or latency. This also implies that the foreperiod effect (or more specifically, the time uncertainty effect) on voluntary and reflexive responding may not be mediated by a single common mechanism.

Third, the effects of foreperiod duration and accessory presence interacted for forearm EMG, but not for reflexive blink EMG. The foreperiod duration effect on the forearm response was reliable only when the accessory was absent, whereas the blink reflex showed facilitation at long warning intervals regardless of whether the accessory was delivered.

Fourth, although accessory presence and increased temporal certainty had similar facilitatory effects on voluntary reaction time and on R50 size and latency, the R80 EMG burst was relatively inhibited in these conditions. This would be less meaningful than the other dissociations, however, if the reciprocal relation between R50 and R80 were merely produced by peripheral refractory effects. For example, if extra motor neurons were recruited for the initial eyelid muscle response (R50) during conditions of phasic alerting, then fewer would have been available when the premotor volley mediating R80 arrived at the facial nucleus. However, a recent experiment examining the reciprocal modulation of R50 and R80 by a visual pre-pulse argues against the refractory hypothesis (Burke and Hackley, 1994). When pre-pulse effects on R80 were examined in two normal subjects who did not exhibit R50, the pattern of modulation for R80 appeared the same as in subjects manifesting both components. Thus, the reciprocal pattern of modulation for R50 and R80 is likely to be due to differences within their central pathways rather than due to peripheral refractory effects (see Hackley and Johnson, 1996, for neuro-anatomical data regarding the central pathways of these components).

An additional dissociation between alerting effects on voluntary and reflexive reactions has been observed in a recent study at this lab. Sollers and Hackley (1993, 1994) presented a visual warning stimulus either 1.5, 3, or 6 s before a reflex eliciting burst of white noise. For one group of subjects, the foreperiods were varied randomly within blocks of trials but, for the other group, the warning intervals were varied between blocks. As in the present study, both reaction time and the blink reflex showed facilitation at longer relative to shorter foreperiods when these intervals were varied randomly from trial to trial. However, for subjects in the blocked group, voluntary and reflexive responses converged. Consistent with prior research using between-block manipulations of foreperiod (e.g., Niemi, 1979), reaction times were relatively facilitated at the shortest foreperiod. By contrast, the acoustic startle blink reflex was most facilitated at the longest foreperiod. An additional dissociation was that postauricular reflexes (onset latency, 11 ms) to the noise bursts showed no reliable variation as a function of foreperiod duration under either the blocked or random conditions.

It is unlikely that such a complex set of findings can be encompassed by any unitary concept of alerting or arousal (cf. Lacey and Lacey, 1970). More likely, the alerting effects triggered by warning and accessory stimuli are mediated by multiple neuromodulatory systems, comprised of brain-stem monoamine and cholinergic pathways. As reviewed by Robbins and Everitt (1995), the reticular formation is now understood to include several subsystems with distinct neuroanatomical, pharmacological, and physiological characteristics. Of special importance in the present context is the recent finding that the nigrostriatal dopamine pathway is critical for temporal uncertainty effects on voluntary responses (Brown and Robbins, 1991). Using an animal model for Parkinson’s disease, the authors found that pharmacological depletion of dopamine in the striatum eliminated RT facilitation at long relative to short foreperiods in a task for which these intervals were manipulated randomly from trial to trial.

Research on humans has also provided evidence regarding the brain mechanisms that underlie temporal uncertainty effects on voluntary reactions. For example, Smolders (1993) compared event-related brain potentials recorded during a choice RT task in blocks of trials with variable versus blocked interstimulus intervals. This manipulation had a 50 ms effect on the time interval from stimulus onset to the onset of the lateralized readiness potential, but had no effect on the interval extending from onset of the lateralized readiness potential to onset of the movement itself. These data appear to rule out a locus for temporal uncertainty effects on low level motor pathways, consistent with the findings of Sollers and Hackley (1993) that the trisynaptic postauricular reflex is unaffected by foreperiod duration. The relatively central locus for temporal uncertainty effects appears more compatible with Posner’s (1978) hypothesis that alerting influences a decision-level mechanism than with Sander’s (1980) motoric hypothesis. However, until the mapping of cognitive stages onto neural processes is better understood, this conclusion must be considered tentative.
For accessory stimulus effects on the masseteric H-reflex, pharmacological investigations in animals have identified the primary neurophysiological mechanism (Stafford and Jacobs, 1990). Norepinephrine secreting neurons located in the lateral tegmentum act upon α-1 noradrenergic receptors in the mesencephalic-V motoneurons to modulate their responsivity to incoming reflexogenic volleys. In humans, an additional mechanism underlying reflex facilitation by an accessory stimulus has been established for both the gastrocnemius H-reflex (Rossignol, 1975) and the trigeminal eyeblink reflex (Boehlouwer et al., 1991; Nakashima et al., 1993). Specifically, the onset latency and duration of the overt reflex to an intense acoustic stimulus were compared with the time course of facilitation by a weak acoustic accessory (i.e. prepulse). Close parallels in the time course of these phenomena indicated that a subliminal reflex to the weak acoustic accessory stimulus can summate with the (supraliminal) response to the intense reflexogenic stimulus, producing facilitation relative to no-accessory control trials. This summation may involve cortical 'long loop' pathways in addition to the direct reflex circuitry (Ligorio-Chauvel et al., 1989).

The close comparability of reflex findings in humans and animals (e.g. Graham, 1975) makes this a promising method for the study of alerting effects in normal and pathological states. If analogs to the alerting effects studied by cognitive psychologists can be identified in the preparations studied by reflexologists, these problems may yield to reductionistic methods in the same manner that associative learning has (e.g. Thompson, 1986).

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5. References


Zeigler, B.L. Priming (match-mismatch) and alerting (modality) effects on reflex startle and simple reaction time. University of Wisconsin, Madison, WI, 1982 (unpublished doctoral dissertation).