

Arousal and activation effects on physiological and behavioral responding during a continuous performance task

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Abstract. Based on previous work indicating different neural substrates, two aspects of energetic state, "arousal" and "activation", have been conceptualized separately in our laboratory. "Arousal" has been defined as the energetic state at any particular time, and task-related "activation" as the task-related change in state from resting baseline to the task situation. Both are reflected in electrodermal activity and measured by skin conductance level. Our previous studies in this area have indicated that physiological responses to stimuli in a task are dependent on the arousal level at the time of stimulus presentation, rather than the task-related activation. In contrast, performance on the task is dependent on the task-related activation, rather than the current arousal level. That is, different aspects of the individual's state determine physiological and behavioral responses. Those studies had examined between-subjects differences in arousal and activation. The present study investigated the relevance of this separation in an across-subjects examination of fluctuations in arousal and activation, and their effects on physiological and behavioral responses, during a continuous performance task. It was found that the magnitude of the phasic orienting reflex to the targets during the task was dependent mainly on arousal, rather than task-related relative activation. Reaction time improved with increasing relative activation, but not with arousal. These findings support our earlier conclusions relating to the usefulness of arousal and activation as distinguishable features of the energetics of physiological and behavioral functions.

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INTRODUCTION

Skin conductance level (SCL) is often used in psychophysiology as an objective measure of the level of arousal (Andreassi 1995), and hence is probably more widely used than any other autonomic nervous system measure. The SCL is a tonic measure which indicates relatively slow fluctuations of bodily states of arousal during emotional, cognitive and physical behavior, expressed in the activity of sympathetic cholinergic neurons at the level of the eccrine dermal sweat glands (Venables and Christie 1980). The skin conductance response (SCR) is a rapid, brief phasic electrodermal response to a single stimulus, which can be considered to be superimposed upon the SCL. It has a simple waveform, and is rather easy to record (Lim et al. 1997, Venables 1991). Regardless of their simple nature, the SCL and SCR contain substantial information that may be related to specific features of brain state and information processing (Lim et al. 1997). Recent studies indicate the close association of central and peripheral measures of arousal. For example, Barry and coworkers (2004) found that the resting SCL was inversely related to alpha power in the EEG, and directly related to alpha frequency. Other studies indicate that the central nervous system regions responsible for generating SCL are also associated with emotional and motivational behavior (Critchley 2002, Damasio 1994). These regions include the hypothalamus and brainstem (e.g., Critchley et al. 2001, 2002, Nagai et al. 2004), amygdala (Asahina et al. 2003, LeDoux 1996, Phelps et al. 2001, Williams et al. 2001), and the orbitofrontal, cingulate and insular cortices (Cechetto and Saper 1990). These data, compatible with the traditional EEG arousal concepts of Sharpless and Jasper (1956) and Cobb (1963), support the use of SCL as a simple measure of CNS arousal.

The phasic orienting reflex (OR), elicited by novel innocuous stimuli, was popularized in the west by Sokolov (1960, 1963a, 1963b), who introduced a new conceptual focus. Sokolov (1963b) stated that the OR reflexively directs attention to the important events occurring in the environment, and hence it may be considered as providing a model of perceptual functioning (Barry 1996, 2006). The OR is an organismic reflex, involving a large range of changes in various physiological systems, and is apparent in a range of physiological measures. Of these, the SCR is the most-widely recognized (Barry 2006). Sokolov (1963a) noted

that repetition of the stimulus results in response decrement or habituation of the OR. Sokolov proposed a comparator theory of habituation, in which a cortical neuronal model of the stimulus, coding information on its parameters, develops with repeated presentations. Each stimulus is compared with the neuronal model, and the discrepancy generates the OR. As a stimulus is repeatedly presented, the model becomes more accurate, the discrepancy decreases, and the response habituates. Within this process, the arousal level of the organism serves as an amplifying factor – the output of the stimulus-comparator stage is amplified by the arousal level – leading to the final output OR (Barry and Sokolov 1993). A similar amplification role for arousal is also included in Groves and Thomson's "dual-process" theory of habituation (Barry 2006). Barry (2004) explored the links between SCL and stimulus-elicited SCRs when stimuli are presented within a task situation. Then, ORs to the stimuli are enhanced and habituation is slowed, but arousal is still involved in OR amplification.

It was suggested previously that arousal and activation may use different neural substrates (Pribram and McGuiness 1975, 1992). Barry and others (2005) followed this suggestion and used "arousal" to refer to the current energetic state, and "activation" to refer to task-related mobilization of arousal. These are both tonic aspects of the energetics dimension. Our conceptualization is that a person is energized/activated during performance of a task, relative to the non-task situation (baseline). Arousal is defined as the current energetic state, and is measured by the current SCL. The increase in energetic state from baseline is defined as activation, and is measured by the change in SCL from baseline to the current task. Barry and coworkers (2005) related the effects of arousal to phasic physiological responses, such as the OR, and the effects of activation to behavior/performance measures, such as reaction time (RT). They used this division to study children's performance in a continuous performance task (CPT). Barry and colleagues (2005) found that the magnitude of the mean phasic OR elicited by target stimuli was dependent on arousal, and the performance measures (mean RT and number of errors) improved with increasing activation. In a follow up study, we used this separation to study adults' performance on a similar task (VaezMousavi et al. 2007). Our findings were in accordance with the previous results and confirmed that arousal and acti-

Energetics of Task-related Performance

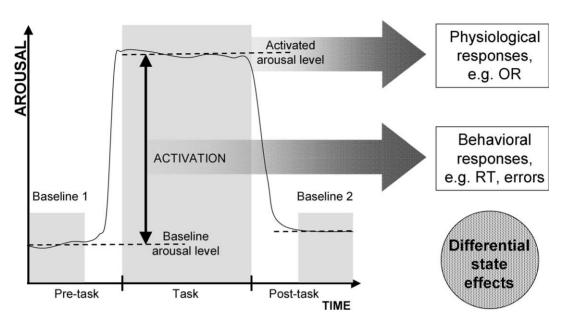


Fig. 1. The present conceptualization distinguishing between "arousal" and "activation" aspects of the energetics dimension is shown. "Arousal" refers to the individual's energetic state at any moment, and is measured by SCL at that time. The task-related "activation" is defined as the change in arousal from resting baseline to the task. During a task, the current (activated) level of arousal affects physiological response amplitudes, while the task-related activation affects behavior/performance on the task.

vation could be usefully separated. This conceptualization is shown in Fig. 1.

These studies of arousal and activation examined between-subjects effects. That is, both Barry and others (2005) and VaezMousavi and coauthors (2007) found that subjects with high current levels of SCL (high arousal) showed larger mean ORs/SCRs to target stimuli in a CPT. This variable did not substantially affect behavioral performance (RT or error rate). In contrast, those subjects who showed a large change in SCL from rest to task (high activation) showed faster responses (both studies) and reduced error rate (Barry et al. 2005). This independent variable did not substantially affect OR/SCR magnitudes.

The present study aimed to advance our understanding of this dichotomy of tonic energetics effects beyond the between-subjects design, by examining the effects of changes in state at each target during the CPT. Our hypothesized link between arousal and physiological response is simple to test – the data from each target stimulus in the CPT can be examined to obtain a mean prestimulus SCL (current/activated arousal level) and mean physiological response (the OR/SCR).

But obtaining a meaningful activation level at each target presents a conceptual problem. Subtracting a subject's mean level of resting baseline SCL from the current/activated arousal level, to obtain activation, results in an activation level perfectly correlated with arousal. This perfect correlation of arousal and activation precludes such a simple approach (which was satisfactory in our previous between-subjects studies because individuals have uncorrelated resting baseline arousal levels). Hence, this study presented two identical sets of target stimuli in succession. We used the second of these sets to provide a series of "baseline" data points instead of using only a single resting baseline. Consequently, to obtain the activation level for each target in the first set, each data point in the second set was subtracted from the corresponding data point in the first set. This provides a series of relative activation scores for the targets in the first set. In terms of our activation hypothesis, we predicted that the relative activation at each target in the first set would determine the difference in reaction time for that target compared to the corresponding target in the second ("baseline") series.

METHODS

Subjects

Twenty-one university students, 17 female and 4 male, aged from 18 to 22 years (mean age 19 years and 5 months) participated in this study. Twenty of the twenty one subjects were right handed. None of the subjects ever suffered an epileptic seizure, serious head injuries, or periods of unconsciousness. None of the subjects had hearing or vision problems, or received treatment for heart/circulation/nerve or sensory problems.

Procedure

Data were collected from each subject in an air-conditioned laboratory, separate from the recording equipment and experimenter. Electrodermal activity was recorded from 7.5 mm diameter Ag/AgCl electrodes on the distal phalanges of the second and third digits of the participant's non-preferred hand, with an electrolyte of 0.05 M NaCl in an inert viscous ointment base.

The subject was presented with a "1-9" variant of the CPT, which presented the digits 0 to 9 as 35 mm by 25 mm numbers on a 35 × 24 cm computer monitor, in a fixed predetermined order based on the Gordon Diagnostic System (Gordon 1986). Each digit was presented for 200 ms, with an 800 ms interstimulus interval. The task consisted of two blocks, presented in succession without a break, each containing 180 stimuli with 15 presentations of the pair "1" followed by "9". The subject was told that the "1" was a warning signal for the target "9", to which he/she was required to respond with a button press. Each block also contained targets not preceded by the cue, as well as cues which were followed by non-targets. Failures to respond to cued targets within 1 000 ms, and responses to target stimuli not preceded by a cue, to non-targets following cues, or responses to other digits, were recorded as errors; such trials were omitted from further analysis. After a practice session, the task commenced when understanding of the instructions was evident. During the CPT, the electrodermal data were recorded continuously at 64 Hz. This procedure was approved by the joint Illawarra Area Health Service/University of Wollongong Human Research Ethics Committee, and all participants provided written informed consent.

Data processing

The mean SCL from the 0.5 s epoch immediately before each target stimulus was calculated as a measure of arousal level for that stimulus. The phasic OR to each target was measured by identifying the SCR with an onset latency between 1 and 3 s following target onset, and determining the phasic change in SCL from response onset to the response peak (Barry 1990). The RT from each response was taken as the behavioral measure of performance. These data were obtained for each target in both the first and second blocks of data. To obtain a measure of the relative activation level for each target in the first block, every SCL in the second block was subtracted from the corresponding value in the first block. Similar differences were calculated to form measures of the relative OR and relative RT

Statistical analysis

In order to describe the overall data pattern in the OR context, scatter plots were first used to examine the effects of trial in the mean SCL, SCR/OR and RT, over all 30 target presentations. Because habituation in the OR context has been associated with exponential trials effects, these data were correlated with log trial number, following Barry and Rushby (2006). Changes in mean SCLs from the first to the second block were tested with a repeated measures analysis of variance. Simple regression analyses were then used to investigate the relationships hypothesized in the Introduction. Arousal effects in the SCR/OR amplitude and RT were examined by regressing these dependent measures for all targets against current SCL. Relative activation effects for the 15 targets in block 1 were examined in the relative ORs and relative RTs, assessed as the difference in these measures at each trial in block 1 relative to block 2. These two dependent variables were regressed on the changes in SCL (from block 2 to block 1) at each trial. If both current SCL and SCL change affected both the physiological or performance dependent variables, their relative importance was assessed using stepwise multiple regression analyses.

RESULTS

Trial effects

As expected, the current SCL decreased significantly over trials, as shown in the top panel of Fig. 2. Each

set of data has been fitted with a logarithmic regression line to indicate the relationship with the independent variable, and the coefficient of determination is included to indicate the strength of that relation. The correlation between current SCL and log trial number was very high (r= -0.979, P<0.001), with these variables sharing 96% of their variance. As shown in the middle panel of Fig. 2, SCR magnitudes also decreased exponentially over trials. There was a high correlation between SCR magnitude and log trial number (r=-0.911, P<0.001), with the variables sharing some 83% of their variance. There was no systematic change in RT over trials (bottom panel of Fig. 2; r=0.002, NS).

Task related activation

The overall SCL was higher in the first block (11.14 μ S) than the second block (10.16 μ S). This difference was statistically significant ($F_{1,14}$ =51.07, P<0.001). Figure 3 shows the difference between SCLs at each target in the two blocks of task presentation. The change in SCL (relative activation) at each target in block 1 was defined as the difference between levels at each target. This measure ranged across trials from 0.40 μ S to 2.01 μ S, with a mean of 0.98 μ S.

Arousal effects

In Fig. 4, the mean SCR amplitude (top panel) and mean RT (bottom panel) are shown for all trials as a function of current SCL, our estimate of arousal. As shown in the top panel, the phasic SCR was directly dependent on the current SCL (r=0.872, P<0.001), with the two variables sharing some 76% of their variance. The bottom panel shows that there was no significant effect of current SCL on RT (r=0.028, NS).

Relative activation effects

The relative SCR and relative RT for each trial in block 1 are shown in relation to the change in SCLs (estimated relative activation levels) in the separate panels of Fig. 5. The top panel shows that the relative SCR was directly dependent on the change in SCL (r=0.663, P<0.01), with the two variables sharing some 44% of their variance. This effect in the relative SCR was similar to, but weaker than, the current SCL effect in the raw SCR amplitudes, explaining 44% of

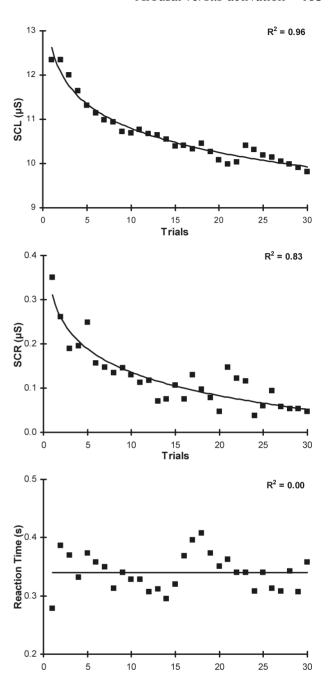


Fig. 2. Variations in SCL, SCR/OR, and RT across trials are depicted. Each set of data in this figure is fitted with a logarithmic regression line, and the coefficient of determination for this regression is indicated. The top panel shows the rapid decrease in SCL from the first to the last trial. Fluctuations in the SCL in some trials are thought to be related to the task difficulty in those trials. The middle panel shows the exponential habituation decrease in SCR/OR magnitude. The third panel shows how the RT in response to the target stimuli fluctuates across the task as a function of task difficulty in some trials. As is readily apparent, the RT variations follow a recurring pattern matching the double presentation of the task.

Trials

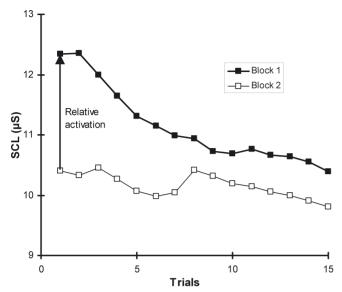


Fig. 3. The SCLs on fifteen trials in the first block of the task presentation (filled squares) are shown in relation to the matching trials in the second block (blank squares). At each trial, the SCL on the second block was subtracted from the SCL on the first block to obtain a measure of task-related relative activation for performance on the first block.

the joint variance compared with 76% for the raw data. The corresponding reduction in the correlation coefficient closely approached statistical significance (Fisher's z=1.57, P=0.058).

The bottom panel of Fig. 5 shows that the relative RT decreased significantly with greater levels of our estimate of relative activation (r=-0.529, P<0.05), an effect explaining some 28% of the variance in these measures.

Arousal versus activation effects in the OR

The above results indicated that, although our estimate of current arousal level (current SCL) strongly determined the SCR/OR to the 30 targets, the estimated relative activation level (change in SCL) also contributed significantly to the relative SCR/OR to the first 15 targets. To determine which of the two independent variables is the more important determinant of the OR, two stepwise multiple regression analyses were carried out. In the first, the raw SCR to the first 15 targets was examined as the dependent variable, and both current SCL and relative SCL were included as independent variables. Only the current SCL was selected as a significant predictor of the phasic SCR ($F_{1,13}$ =47.12, P<0.001); relative SCL was excluded from the analysis (F<1). In the second, the relative

SCR to the first 15 targets was examined as the dependent variable, and current SCL and relative SCL were again included as independent variables. Only the current SCL, our measure of arousal level, was selected as a significant predictor of the relative SCR/OR ($F_{1,13}$ =11.42, P<0.005); relative SCL (our measure of activation) was excluded from the analysis (F<1).

DISCUSSION

The across subjects/between trials approach used in the present study allowed for a new focus of attention on arousal and activation during a CPT. Using one block of the task as a "baseline" to establish relative activation in another block, we explored variations in our estimates of arousal (current SCL) and relative activation (activated SCL – baseline SCL) from trial to trial, and examined their effects on the dependent variables.

The overall SCL decreased dramatically across trials. The maximum SCL recorded was 12.91 μ S for the first trial, and the minimum was 10.21 μ S for the last trial, some 26.5% reduction in level. This decrease is readily understood as an exponential decrease in arousal level (e.g., Raskin 1973) with stimulus repetition in a task period. It is directly comparable with the trials effects in SCL observed with a single repetitive stimulus in Barry and Sokolov (1993).

Trial-by-trial fluctuations in SCL are apparent in Fig. 2, superimposed on the orderly decline with trials. These fluctuations probably reflect differences in task difficulty due to particular combinations of distracter stimuli. The Gordon Diagnostic System version of the CPT (Gordon 1986), that we used as a basis for our stimulus sequence, was developed to aid in the diagnosis of Attention-Deficit/Hyperactivity Disorder in children. For that purpose, fluctuations in task difficulty were deliberately set up and used to provoke different kinds of omission and commission errors, which are helpful in the diagnostic process. For our present purpose, they provide more variability than would be apparent in a randomized presentation order, as might commonly be used in laboratory research. Further, the use of a fixed stimulus order (essential in a normed commercial instrument such as the Gordon Diagnostic System) allowed us to use across-subject averaging to clarify meaningful trial-by-trial effects. The overall significant decrease in SCL (arousal level) from the first block in the task to the second, and similar SCL

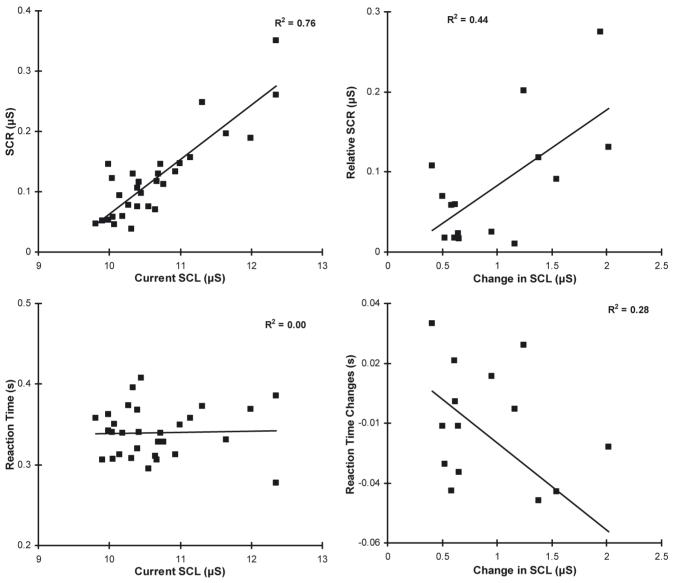


Fig. 4. The mean amplitude of the SCR/ORs (top panel) and RTs (bottom panel) are plotted as a function of current SCL (arousal level). Data have been fitted with linear regression lines, and the coefficient of determination for this regression is indicated.

Fig. 5. The mean amplitudes for relative SCR/ORs (top panel) and relative RTs (bottom panel) as a function of the difference in SCLs from block 2 to block 1 (relative activation). The relationship in the top panel is not as strong as the corresponding relationship in the top panel of Fig. 4.

fluctuations in both blocks, supports the concept of using the second block's SCL as the baseline measures.

The OR also decreased exponentially across the task. The maximum amplitude of the OR was in the first trial (0.35 μ S) and it decreased substantially over trials (to 0.04 μ S). The decrement of the SCR across the task, which is shown in Fig. 2, can be readily attributed to habituation of the phasic OR to the target stimuli (Barry 1990, 2004, Barry and Sokolov 1993, Barry et al. 1993). As is clearly apparent in the bottom panel

of Fig. 2, RT followed a non-habituating pattern which repeated in the second block. One may relate the longer RTs to more difficult trials, and the shorter RTs to the easier trials.

The phasic OR amplitudes to the target stimuli in the CPT correlated strongly with arousal. This effect was stronger than the correlations found in previous between-subject studies (Barry et al. 2005, VaezMousavi et al. 2007). The relative OR was also correlated with relative activation, but this correlation

was not as strong. The stepwise multiple regressions showed that the current arousal level, rather than relative activation, was the significant predictor of the phasic OR, whether in absolute or relative terms. This major dependence of the OR on arousal level was similar to previous findings from this laboratory (Barry 2004, Barry and Sokolov 1993, Barry et al. 2005, VaezMousavi et al. 2007). This result confirms our conceptualization that the current arousal level operates as an amplifier of the phasic OR elicited during the CPT (Barry et al. 2005). This is in accordance with the amplifying role attributed to arousal in both Sokolovian and dual-process theories of OR evocation and habituation (Barry 2006).

Unlike our previous between-subject studies, no negative activation was observed in the present investigation. The negative activation had been ascribed to the employment of an unsatisfactory baseline level (Barry et al. 2005, VaezMousavi et al. 2007). In this regard, the new approach to determining baseline SCLs on a pertarget basis appears very useful. The measure of taskrelated activation had been previously found to determine behavioral efficiency in terms of RT (Barry et al. 2005, VaezMousavi et al. 2007). Results in the present study confirm the previous findings, as we found a significant correlation between the relative activation on a trial-by-trial basis over the task and improvement in RT. In contrast, arousal levels had no effect on RT. These results provide important support for our previous findings (Barry et al. 2005, VaezMousavi et al. 2007), and also for our hypotheses in the present study.

Although the research reported in this study focused on the electrodermal system, using SCL as the "gold standard" in the measurement of arousal, another line of our research is attempting to clarify the CNS correlates of the energetics dimension. It was noted earlier that we have established global power in the traditional EEG alpha band as a correlate of eyes-closed resting state SCL (Barry et al. 2004). These two measures have an inverse relationship, with increased SCL associated with reduced alpha power. That study linked together traditional autonomic (e.g., Barry and Sokolov 1993) and EEG (e.g., Cobb 1963) concepts of arousal.

Arousal *versus* activation effects, as conceptualized in our model (Fig. 1), have not been explored in the traditional EEG literature, but it is generally accepted that many tasks produce focal EEG activations over the brain areas involved. For example, Rebert and colleagues (1978) and Harmony and others (1990) have

associated text reading with increased activity in the parietal areas. Thus specific tasks may be expected to produce both reduced global alpha and focal EEG changes topographically dependent on the cortical areas involved in the task processing. In relation to our model, only the global alpha change is linked to the electrodermal change we associate with the energetics dimension; the focal EEG changes reflect non-energetic stimulus and response processing.

We recently reported supportive data associated with the simple change from eyes-closed to eyes-open conditions (Barry et al. 2007). The eyes-open condition was associated with an increase in SCL and a decrease in global alpha power, both interpreted as indicating an increase in arousal. There were also focal changes in the other traditional EEG bands: reduced lateral frontal delta and posterior theta, and decreased posterior (but increased frontal) beta. We associate these specific focal changes with visual processing, rather than simple arousal increases. Further work, exploring the separation of the arousal changes in global alpha activity from such task-specific focal processing effects, is in progress.

Generally, the outcome of the across subject/between trials analyses of the present study support the earlier suggestions conceptualizing arousal and activation independently. We found that the current arousal level (as measured by current SCL) significantly affected OR magnitude, but not the RT in the CPT. Relative activation in the CPT (as measured by the activated – baseline change in SCL) affected RT in the task, as well as the OR to the target stimuli. The latter effect was not as strong as the raw arousal effect. Thus current arousal was shown to be the major determinant of the physiological response to the targets, and relative activation was the sole determinant of the relative RT to the targets. These findings support the previous arousal/activation findings from this laboratory and the conceptualization shown in Fig. 1.

CONCLUSIONS

These findings confirm our separation of the tonic energetics dimension into arousal and activation. The former is the major energetics variable influencing physiological responding, and the latter is the major energetics variable affecting behavioral performance, such as RT. This confirmation may be valuable in reinvigorating our perception of the role of the energetics dimension in understanding physiological responding

and behavioral performance in relation to task-related stimulus events. The future direction of our research in this area will include the examination of these findings in a within-subject investigation. Following this line of exploration in relation to skilled activities (for example sport performance) and other aspects of individual differences, may well be productive.

REFERENCES

- Andreassi JL (1995) Psychophysiology: Human behavior and physiological response. Third edition. LEA, New Jersey.
- Asahina M, Suzuki A, Mori M, Kanesaka T, Hattori T (2003) Emotional sweating response in a patient with bilateral amygdala damage. Int J Psychophysiol 47: 87–93.
- Barry RJ (1990) Scoring criteria for response latency and habituation in electrodermal research: A study in the context of the orienting response. Psychophysiology 27: 94–100.
- Barry RJ (1996) Preliminary Process Theory: Towards an integrated account of the psychophysiology of cognitive processes. Acta Neurobiol Exp (Wars) 56: 469–484.
- Barry RJ (2004) Stimulus significance effects in habituation of the phasic and tonic orienting reflex. Integ Physiol Behav Sci 39: 166–179.
- Barry RJ (2006) Promise versus reality in relation to the unitary orienting reflex: A case study examining the role of theory in psychophysiology. Int J Psychophysiol 62: 353–366.
- Barry RJ, Rushby JA (2006) An orienting reflex perspective on anteriorisation of the P3 of the event-related potential. Exp Brain Res 173: 539–545.
- Barry RJ, Sokolov EN (1993) Habituation of phasic and tonic components of the orienting reflex. Int J Psychophysiol 15: 39–42.
- Barry RJ, Feldmann S, Gordon E, Cocker KI, Rennie C (1993) Elicitation and habituation of the electrodermal orienting response in a short interstimulus interval paradigm. Int J Psychophysiol 15: 247–253.
- Barry RJ, Clarke AR, McCarthy R, Selikowitz M, Rushby JA, Ploskova E (2004) EEG differences in children as a function of resting-state arousal level. Clin Neurophysiol 115: 402–408.
- Barry RJ, Clarke AR, McCarthy R, Selikowitz M, Rushby JA (2005) Arousal and activation in a continuous performance task: An exploration of state effects in normal children. J Psychophysiol 19: 91–99.
- Barry RJ, Clarke AR, Johnstone SJ, Magee CA, Rushby JA (2007) EEG differences between eyes-open and eyes-

- closed resting conditions. Clin Neurophysiol 118: 2765–2773.
- Cechetto DR, Saper CB (1990) Role of the cerebral cortex in autonomic function. In: Central Regulation of Autonomic Functions (Loewy AD, Spyer KM, Eds). Oxford Univ. Press, Oxford, UK, p. 208–223.
- Cobb WA (1963) The normal adult EEG. In: Electroencephalography (Hill D, Parr G, Eds). Macmillan, New York, p. 232–249.
- Critchley HD (2002) Electrodermal responses: What happens in the brain? Neuroscientist 8: 132–142.
- Critchley HD, Melmed RN, Featherstone E, Mathias CJ, Dolan RJ (2001) Brain activity during biofeedback relaxation. A functional neuroimaging investigation. Brain 124: 1003–1012...
- Critchley HD, Melmed RN, Featherstone E, Mathias CJ, Dolan RJ (2002) Volitional control of autonomic arousal: A functional magnetic resonance study. Neuroimage 16: 909–912.
- Damasio AR (1994) Descartes' Error: Emotion, Reason, and the Human Brain. Grosset Putnam, New York.
- Gordon M (1986) How is a computerised test used in the diagnosis of attention deficit disorder. J Child Contemp Soc 19: 53–64.
- Harmony T, Hinojosa G, Marosi E, Becher J, Rodriguez M, Reyes A, Rocha C (1990) Correlation between EEG spectral parameters and an educational evaluation. Int J Neurosci 54: 147–155.
- LeDoux JE (1996) The Emotional Brain: The Mysterious Underpinnings of Emotional Life. Simon and Schuster, New York.
- Lim CL, Rennie C, Barry RJ, Bahramali H, Lazzaro I, Manor B, Gordon E (1997) Decomposing skin conductance into tonic and phasic components. Int J Psychophysiol 25: 97–109.
- Nagai Y, Critchley HD, Featherstone E, Trimble MR, Dolan RJ (2004) Activity in ventromedial prefrontal cortex covaries with sympathetic skin conductance level: A physiological account of a "default mode" of brain function. Neuroimage 22: 243–251.
- Phelps EA, O'Connor KJ, Gatenby JC, Gore JC, Grillon C, Davis M (2001) Activation of the left amygdala to a cognitive representation of fear. Nat Neurosci 4: 437–441
- Pribram KH, McGuiness D (1975) Arousal, activation, and effort in the control of attention. Psychol Rev 82: 116–149.
- Pribram KH, McGuiness D (1992) Attention and para-attentional processing. Event-related brain potentials as tests of a model. Ann N Y Acad Sci 658: 65–92.

- Raskin DC (1973) Attention and arousal. In: Electrodermal Activity in Psychological Research (Prokasy WF, Raskin DC, Eds). Academic Press, New York, London.
- Rebert C, Wexler B, Sproul A (1978) EEG asymmetry in educationally handicapped children. Electroencephalogr Clin Neurophysiol 45: 436–442.
- Sharpless S, Jasper H (1956) Habituation of the arousal reaction. Brain 79: 655–680.
- Sokolov EN (1960) Neuronal models and the orienting reflex. In: The Central Nervous System and Behavior: Transactions of the 3rd Conference (Brazier MA, Ed.). Macy, New York, p. 187–276.
- Sokolov EN (1963a) Higher nervous functions: The OR. Ann Rev Physiology 25: 545–580.
- Sokolov EN (1963b) Perception and the Conditioned Reflex. Pergamon, Oxford.

- VaezMousavi SM, Barry RJ, Rushby JA, Clarke AR (2007) Evidence for differentiation of arousal and activation in normal adults. Acta Neurobiol Exp (Wars) 67: 179–186.
- Venables PH (1991) Autonomic activity. Ann N Y Acad Sci 620: 191–207.
- Venables PH, Christie MJ (1980) Electrodermal activity. In: Techniques in Psychophysiology (Martin I., Venables PH, Eds). John Wiley and Sons Ltd., London, p. 3–67.
- Williams LM, Phillips ML, Brammer MJ, Skerrett D, Lagopoulos J, Rennie C, Bahramali H, Olivieri G, David AS, Peduto A, Gordon E (2001) Arousal dissociates amygdala and hippocampal fear responses: evidence from simultaneous fMRI and skin conductance recording. NeuroImage 14: 1070–1079.

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