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Trends in
Cognitive Sciences

Spotlight

Arousal and performance: revisiting the famous inverted-U-shaped curve

Sander Nieuwenhuis [1,*]

Arousal level is thought to be a key determinant of variability in cognitive performance. In a recent study, Beerendonk, Mejías *et al.* show that peak performance in decision-making tasks is reached at moderate levels of arousal. They also propose a neurobiologically informed computational model that can explain the inverted-U-shaped relationship.

There is growing interest in the often-large impact of spontaneous fluctuations in brain state on cognitive functions [1]. This has led researchers to revisit the classic Yerkes-Dodson law [2], which describes a curvilinear relationship between arousal level and cognitive performance (Box 1). Although this 'law' is covered in many introductory psychology textbooks and widely cited on stress-management websites, surprisingly few studies have investigated the shape of the arousal–performance relationship in humans. In a new study, Beerendonk, Mejías *et al.* [3] report the most extensive empirical study to date and additionally propose a computational model that can explain this relationship.

It is difficult to assess performance over a wide range of arousal states, not only because this requires a large number of observations, but also because human participants (as opposed to rodents) are unlikely to visit extreme arousal states during a typical cognitive psychology experiment. As a result, researchers may find a linear relationship even when the true relationship has an inverted-U shape. Beerendonk, Mejías *et al.* [3] addressed this challenge by collecting around 3500 trials per participant in a variety of tasks over the course of several hours. The participants performed a series of six perceptual decision-making tasks in which they had to detect or discriminate between auditory or visual stimuli presented against a background of noise. In all tasks, the signal-to-noise ratio was titrated to reach 75% accuracy. Task performance was related to spontaneous fluctuations in pretrial pupil size, a popular index of arousal and brain state.

When all 3500 trials were combined and divided into 20 equally populated bins on the basis of pretrial pupil size, perceptual sensitivity (d-prime) showed a negative quadratic (inverted-U-shaped) relationship with arousal. When the arousal–performance data were plotted separately for detection and discrimination tasks, and separately for auditory and visual tasks, in each case model comparisons also favored a negative quadratic over a linear relationship. These relationships remained largely intact after time-on-task effects were statistically removed. Response times also consistently showed a quadratic relationship with arousal, with the fastest response times occurring during periods of intermediate pupil size. Altogether, quadratic arousal–performance relationships seem to be a robust property of perceptual decision-making tasks in humans.

To understand this relationship, Beerendonk, Mejías *et al.* [3] developed a neurobiologically informed computational model. The core of the model is a well-studied biophysically realistic cortical network model of decision-making [4]. This consists of two evidence accumulators (populations of excitatory neurons), each encoding a specific perceptual decision (e.g., 'target present' vs. 'target absent'), which compete with each other through feedback inhibition from a population of interneurons. The combination of sensory input and recurrent feedback inhibition leads one of the accumulators to produce a categorical choice through winner-take-all competition. Building on this model, the researchers assumed that an arousal signal would influence both evidence accumulators equally through its effects on two additional populations of inhibitory interneurons expressing somatostatin (SST) and vasoactive intestinal peptide (VIP). The population of SST neurons directly inhibited the evidence accumulators, whereas the population of VIP neurons inhibited the SST population, thus (indirectly) disinhibiting the evidence accumulators.

When the authors let the model perform the task under a range of arousal levels, the simulated results showed an inverted-U-shaped relationship between arousal and perceptual sensitivity, mimicking the empirical results. A study of the internal model dynamics revealed that at low arousal levels, the two accumulators were slightly suppressed and therefore relatively insensitive to sensory input, leading to poor task performance. As arousal levels grew, thus increasing VIP firing and (indirectly) suppressing SST firing, the accumulators became disinhibited and more and more sensitive to sensory input. This trend was maintained until a critical point at which VIP firing saturated while SST firing continued to increase with arousal. This did the trick: the inhibitory effect of the SST population on the evidence accumulators gradually started to outweigh the disinhibitory effect of the VIP population, leading the accumulators to return to the slightly suppressed, suboptimal state. Thus, the peak of the resulting inverted-U-shaped arousal–performance curve corresponded with the arousal level at which VIP firing saturated.

Beerendonk, Mejías, and colleagues stress that their model should be considered tentative because it relies on a

Box 1. Yerkes-Dodson law or Hebb's curve?

Yerkes and Dodson (1908) [2] are often given credit for a 'law' describing the relationship between arousal and task performance, but they did not measure arousal nor collect a typical performance measure. Instead, their original paper examined the speed with which mice learnt to discriminate between two boxes, one bright, one darker, on the basis of electrical shocks administered when they chose the wrong box. The experimenters varied the strength of the shocks and the difficulty of the discrimination task. The results, based on two to four mice per condition, showed that the optimal shock level decreased with increasing task difficulty (Figure I). For many decades, it was this finding, later replicated in other species, that researchers referred to as the Yerkes-Dodson law. However, this changed in the 1950s, when researchers became mesmerized by the two U-shaped curves in the original figure and started to refer to this curvilinear relationship as the Yerkes-Dodson law [5]. While Yerkes and Dodson acknowledged the restricted scope of this 'law', researchers in the 1950s started to project onto the two axes other constructs than strength of shock and learning speed, such as motivation, drive, and performance. The proponents of these new psychological theories seemed to have forgotten about the linear effect in the easy condition and may not have known about a re-analysis of the Yerkes-Dodson data, showing that the curvilinear effect in the difficult condition became linear if an alternative definition of learning speed was chosen [5]. In the years after the first studies of the ascending reticular activating system, which regulates central arousal, the psychological concept of arousal replaced the more traditional *x*-axis concepts of motivation and drive. It was Hebb [10] who first proposed an inverted-U-shaped relationship between arousal and performance. 'Hebb's curve' would therefore be a more appropriate name for this relationship.

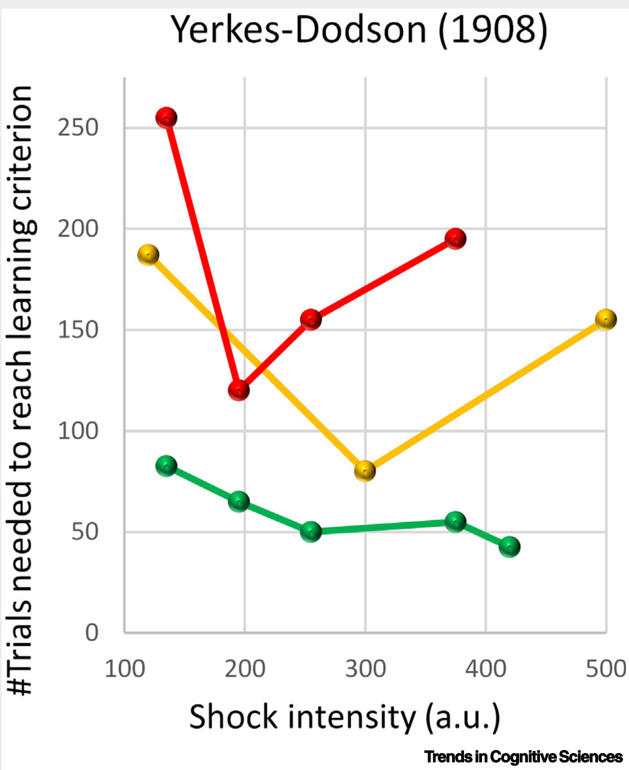

Figure I. Original data reported by Yerkes and Dodson (1908) [2].

number of important neurobiological assumptions, some of which require empirical validation. Testing these assumptions requires the use of invasive electrophysiological and optogenetic methods in animal models. However, even if some of the critical assumptions are invalidated, the modeling work of Beerendonk, Mejías, and colleagues sets a new standard for future studies that aim to understand the relationship between arousal and performance.

The model of Beerendonk, Mejías, *et al*. [3] is faced with three important challenges. First, in the work presented, the model predicts that optimal performance is always reached at the same level of arousal. However, previous studies have found that the optimal arousal level depends on task difficulty and is higher for easier tasks [5,6]. It is unclear whether the model can account for these observations. Second, the model is only able to simulate results for relatively simple decision-making tasks. Significant modifications would be needed to simulate the Yerkes-Dodson law for more complex tasks. Third, unlike other theories of arousal, the model of Beerendonk, Mejías *et al*. does not (yet) address the functional significance of high arousal levels. Easterbrook's [7] cue-utilization theory proposed that at high arousal levels, people can pay attention to, or process, only a limited set of stimuli. This often hampers performance on typical cognitive psychology experiments but can be highly beneficial in stressful (i.e., high-arousal) situations, because it allows individuals to focus their attention on the most urgent and vital information and take rapid action [5]. In a similar vein, the arousal-biased competition theory assumes that high phasic arousal enhances the processing of task-relevant or otherwise salient information, but impairs processing of low-priority information [8]. Finally, the adaptive gain theory proposes that high tonic arousal impairs performance on the specific task at hand, but promotes attentional disengagement and exploration, thus facilitating escape from stressful situations [9].

The innovative work by Beerendonk, Mejías, and colleagues contributes to mounting evidence suggesting that cognitive performance strongly depends on brain state. Further developments of their model could address the context dependence of optimal arousal level as well as the link with existing arousal theories.

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Declaration of interests

No interests are declared.

[1]Institute of Psychology, Leiden University, Wassenaarseweg 52, 2333 AK Leiden, the Netherlands

*Correspondence:
snieuwenhuis@fsw.leidenuniv.nl (S. Nieuwenhuis).

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