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Research report

Modulation of attention and stress with arousal: The mental and physical effects of riding a motorcycle

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ABSTRACT

Existing theories suggest that moderate arousal improves selective attention, as would be expected in the context of competitive sports or sensation-seeking activities. Here we investigated how riding a motorcycle, an attention-demanding physical activity, affects sensory processing. To do so, we implemented the passive auditory oddball paradigm and measured the EEG response of participants as they rode a motorcycle, drove a car, and sat at rest. Specifically, we measured the N1 and mismatch negativity to auditory tones, as well as alpha power during periods of no tones. We investigated whether riding and driving modulated non-CNS metrics including heart rate and concentrations of the hormones epinephrine, cortisol, DHEA-S, and testosterone. While participants were riding, we found a decrease in N1 amplitude, increase in mismatch negativity, and decrease in relative alpha power, together suggesting enhancement of sensory processing and visual attention. Riding increased epinephrine levels, increased heart rate, and decreased the ratio of cortisol to DHEA-S. Together, these results suggest that riding increases focus, heightens the brain's passive monitoring of changes in the sensory environment, and alters HPA axis response. More generally, our findings suggest that selective attention and sensory monitoring seem to be separable neural processes.

1. Introduction

The advent of portable, light-weight electroencephalography (EEG) systems has opened the doors to a new era of research, fostering ecological validity and exploration of system interactions (Ladouce et al., 2016). Supporting the use of mobile EEG for research, validation studies have shown that event-related potential (ERP) effects are preserved despite changes in noise characteristics (Scanlon et al., 2017, 2019a, 2019b). Specifically, studies have replicated ERP effects across a variety of metrics, including test–retest reliability (Malcolm et al., 2019), topography and morphology for oddball-elicited parietal P3 (Linden, 2005; Polich, 2007), and frontal mismatch-negativity (Näätänen et al., 2007); across indoor versus outdoor activities (Debener et al., 2012; Scanlon et al., 2017, 2019a, 2019b); and across stationary versus mobile conditions, specifically walking (Debener et al., 2012; De Vos et al., 2014; De Vos and Debener, 2014; Gramann et al., 2010) and biking (Scanlon et al., 2017, 2019a, 2019b; Zink et al., 2016). Emerging studies using mobile EEG are revealing system interactions that were inaccessible in a lab setting, including those between motion and visual processing (Ladouce et al., 2019; Liang et al., 2018; Reiser et al., 2019), sensory tuning with natural noise (Scanlon et al., 2019a, 2019b), as well as episodic encoding and spatial context (Griffiths et al., 2016; Park and Donaldson, 2019; Piñeyro Salvidegoitia et al., 2019).

Here we were interested in leveraging mobile EEG to test a well established, but only partially validated, interaction between attention and arousal. Several lines of evidence suggest that moderate arousal

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facilitates performance – in both physical and cognitive realms (Krahenbuhl, 1975; Schmidt-Kassow et al., 2013) – through putative mediation by the locus coeruleus-norepinephrine (LC-NE) system (Mefford and Potter, 1989; Solanto, 1998). Specifically, arousal is thought to modulate the gain of neural responses to target, or selectively predisposed, inputs (Eldar et al., 2013; Warren et al., 2016), thus facilitating selective attention (Aston-Jones and Cohen, 2005; Nieuwenhuis et al., 2011; Sara and Bouret, 2012; van den Brink et al., 2016). This interaction is particularly interesting in the context of competitive sports (Krahenbuhl, 1975) and sensation-seeking activities (Ball and Zuckerman, 1992), such as skydiving or motorcycle riding, in which arousal-based facilitation of performance is associated with positive sensations and anecdotal reports of stress-relief, relaxation, and heightened sensory perception. The aforementioned empirical and theoretical data from laboratory experiments predict that arousing activities heighten sensory processing, leading to a positive subjective response that may contribute to the paradoxical co-occurrence of risk and self-reported stress-relief in sensation-seeking activities. The extant literature, however, has not documented the precise nature of this effect on sensory processing or the extent of associated arousal or stress-relief.

We used a combination of EEG and hormonal assays to monitor sensory and physiological responses during motorcycle riding, an activity particularly well suited to testing these hypotheses, as riders' safety and enjoyment require acute and dynamic control of attention. This approach allowed us to address two previously untested questions: whether arousal during motorcycle riding facilitates selective attention, thus increasing focus and suppressing distractions, as predicted by existing theoretical frameworks of the LC-NE system (Aston-Jones and Cohen, 2005; Sara and Bouret, 2012); and whether riding facilitates sensory monitoring, as would be expected based on self-reports of heightened perception.

We evaluated selective attention and sensory monitoring with an auditory oddball task, not only because it is well-validated in the context of mobile EEG (Debener et al., 2012; Scanlon et al., 2017, 2019a, 2019b) but also because auditory tones are a reliable tool for the passive probing of sensory and attention processing during riding (Näätänen et al., 2007, 2011). Namely, primary auditory cortex responses to tones arise approximately 100 ms after tone onset and appear as distinct negative peaks in the EEG signal (N1). The listener's attention can modulate this response in two ways. First, the response is stronger if the listener attends closely to the auditory tones and is weaker if the listener ignores the tones. If the act of riding a motorcycle focuses the rider's attention on visual cues, at the expense of auditory cues, then we would expect a reduced auditory response while riding (Alain and Arnott, 2000; Sussman, 2007). Second, the N1 response following sudden changes in the auditory environment (e.g., a sudden noise from a glass shattering in an already-noisy cafeteria) deviates from the N1 response following a standard tone – a difference known as the mismatch-negativity (MMN) (Garrido et al., 2009; Näätänen et al., 2007). Critically, this effect is thought to occur pre-attentionally (and automatically), as it is reliable even if the listener is not attending to the tones. Thus, if motorcycle riding is accompanied by heightened sensory monitoring, we expect riding to increase sensitivity to the unexpected tone and, thus, to increase the magnitude of the MMN.

One limitation with the use of the auditory oddball task to measure *selective attention* is that it provides an *indirect* metric of inferred reduced auditory processing, rather than a direct metric of enhanced visual attention expected during riding. To obtain such a direct metric we thus included measures of spectral power in the alpha-range (8–12 Hz) across posterior electrodes, during the auditory trials. Notably, modulations of posterior alpha power have been associated reliably with visual attention, thought to reflect mechanisms that gate sensory inputs (Foxe and Snyder, 2011; Jensen and Mazaheri, 2010; Klimesch, 2012; Pfurtscheller et al., 1996; da Silva and da Silva, 1991). Power *increases* have been related to blocking of sensory signals and *decreases* to engagement with sensory content, reliably documented in perception (Busch et al., 2009; Hanslmayr et al., 2007; Samaha and Postle, 2015), selective attention (Foxe and Snyder, 2011; Jensen and Mazaheri, 2010), working memory (Jensen, 2002; Sauseng et al., 2005) and memory encoding (Klimesch, 1997, 2012). Further, the large amplitude of the alpha signal (Adrian and Matthews, 1934; Pfurtscheller et al., 1996), its within-subject reliability (Krause et al., 2001; McEvoy et al., 2000; Näpflin et al., 2007; Neuper et al., 2005; Tenke et al., 2017), and its generalizability across species (cat, dog, primate, rat, guinea pig (Hughes and Crunelli, 2005; Steriade et al., 1990)), supports its candidacy as a marker of visual attention during riding. Specifically, an increase in visual attention during riding would be expected to decrease alpha power across posterior electrodes.

Riding a motorcycle is demanding of the body's homeostasis (Konttinen et al., 2008); when homeostasis is challenged or disturbed, stress results. Such disturbance or challenge stimulates the short-timed peripheral sympathetic/adrenomedullary (SAM) system followed by the release of catecholamines, and the prolonged-timed response by hypothalamic–pituitaryadrenal (HPA) axis leading to increasing levels of serum glucocorticoids (and other hormones) (Khansari et al., 1990). However, depending on the magnitude of the stressful event, duration (minutes, hours, or days), coping behavior, and mind-body's resilience, the responses of the SAM system and HPA axis differ, which will reflect on the changes in the secretion of catecholamines and glucocorticoids (Bosch et al., 2001; Matalka, 2003; Seery, 2011). Therefore, for an objective assessment of the subjective experience of motorcycle riding, we measured physiological responses that are reflected by the changes in SAM (heart rate and epinephrine) and HPA axis (cortisol, dehydroepiandrosterone-sulphate (DHEA-S), and testosterone level (Buford and Willoughby, 2008; Morgan et al., 2004; Pakanen et al., 2016; Ritsner et al., 2004; Warnock et al., 2010) across experimental conditions.

This study thus directly tests existing hypotheses regarding attention/arousal system interactions and, concurrently, employs multiple ecologically-valid measures to quantify the subjective experience of motorcycle riding.

2. Results

2.1. Eeg

We consider first the N1 magnitude, averaged across standard and oddball tones, at electrode Fz ($\mu_{riding} = -0.6$ uV, $\mu_{driving} = -1.2$ uV, $\mu_{stationary} = -1.3$ uV). There was a significant effect of condition on the N1 magnitude ($F(2,80) = 20.35$, $p < 10^{-7}$). A post hoc *t*-test revealed that the N1 was reduced significantly while riding relative to the stationary condition ($\mu_{riding\ -\ stationary} = 0.62$, $t(41) = 4.36$, $p_{corrected} < 10^{-3}$). The N1 magnitude also was reduced during riding than during driving ($\mu_{riding\ -\ driving} = 0.61$, $t(40) = 4.74$, $p_{corrected} < 10^{-4}$). The N1 during driving did not differ from the stationary condition ($\boldsymbol{\mu}_{driving\ -\ stationary} = 0.06$, $t(40) = 0.84$, $p_{corrected} = 0.41$). Fig. 1A and B show ERPs for representative electrodes.

We next consider the MMN magnitude at electrode Fz ($\mu_{riding} = -0.38$ uV, $\mu_{driving} = -0.11$ uV, $\mu_{stationary} = -0.24$ uV). There was a significant effect of condition on MMN ($F(2,78) = 3.6$, $p = 0.032$). A post hoc *t*-test revealed that the MMN magnitude increased while riding, relative to the non-riding (driving and stationary) conditions ($\mu_{riding\ -\ non\text{-}riding} = -0.2$, $t(39) = 1.15$, $p = 0.041$). Fig. 1C illustrates the whole-brain response 100 ms after the onset of the oddball tone.

We report here the relative spectral power in the alpha frequency band at selected posterior electrodes during the period of no tones ($\mu_{riding} = 4.7\%$, $\mu_{driving} = 5.2\%$, $\mu_{stationary} = 5.1\%$). There was a significant effect of condition on relative alpha power ($F(2,76) = 21.39$, $p < 10^{-7}$, Fig. 2A). Relative alpha power was less while riding than while stationary ($\mu_{riding\ -\ stationary} = -0.41$, $t(39) = 5.2$, $p < 10^{-4}$, Fig. 2B), no different while driving than while stationary ($\mu_{driving\ -\ stationary} = 0.17\%$, $t(39) = 1.87$, $p = 0.07$), and less while riding than while driving ($\mu_{riding\ -}$

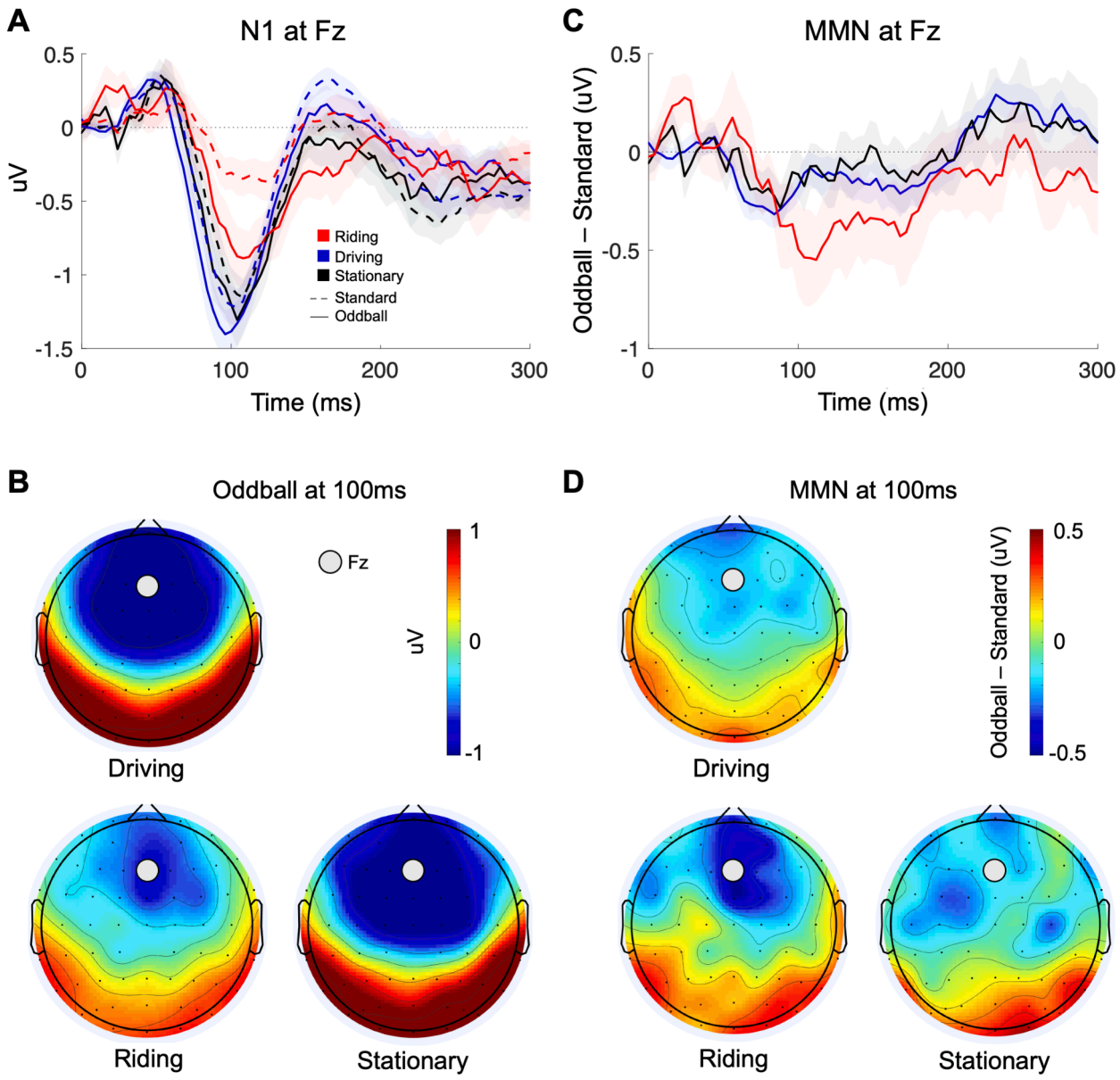

Fig. 1. ERP Results. A. Event-related potentials at Fz in response to standard and oddball tones in driving, riding, and stationary conditions. Shaded areas represent standard error of the mean. B. The whole-brain response to the oddball tone 100 ms after its onset in each of the three conditions, showing significantly less response to tones while riding. C. MMN at Fz in driving, riding, and stationary conditions. Shaded areas represent standard error of the mean. D. The whole-brain MMN response (oddball – standard) 100 ms after tone onset in each of the three conditions, showing that part of the frontal lobe was significantly more responsive to oddball tones while riding.

$_{driving} = -0.56\%$, $t(39) = 5.88$, $p < 10^{-5}$).

2.2. Heart rate

After data exclusion due to electrode detachment, excessive noise, and acquisition errors, we retained usable EKG data from 38 participants ($\mu_{riding} = 84$ BPM, $\mu_{driving} = 78$ BPM, $\mu_{stationary} = 74$ BPM). Data from the riding condition were not distributed normally (Shapiro-Wilks test, $p = 0.02$); thus, we applied the natural logarithm to all conditions to normalize the distribution before conducting significance tests. There was a significant effect of condition on mean heart rate ($F(2,70) = 32.5$, $p < 10^{-9}$). All pairwise comparisons differed from chance significantly (Fig. 3A): heart rate was greater while riding than while stationary ($\mu_{riding\ -\ stationary} = 9.9$ BPM, $t(35) = 6.4$, $p_{corrected} < 10^{-6}$), greater while driving than while stationary ($\mu_{driving\ -\ stationary} = 3.9$ BPM, $t(35) = 3.9$, $p_{corrected} < 10^{-3}$), and greater while riding than while driving ($\mu_{riding\ -}$ $_{driving} = 6.0$ BPM, $t(35) = 5.1$, $p_{corrected} < 10^{-4}$).

2.3. Hormones

We collected urine data from 43 participants and salivary data from 47 participants. One participant's urine sample in the riding condition was too dilute, and one participant's salivary sample in the driving condition was collected improperly. These samples were excluded from analysis, reducing the number of samples in the riding urine test and driving salivary test to 42 and 46, respectively. On the remaining samples, we obtained descriptive statistics for epinephrine ($\mu_{riding} = 14.6$ μg/g Cr, $\mu_{driving} = 12.4$ μg/g Cr, $\mu_{stationary} = 11.3$ μg/g Cr), testosterone ($\mu_{riding} = 49.7$ pg/mL, $\mu_{driving} = 47.8$ pg/mL, $\mu_{stationary} = 48.4$ pg/mL), cortisol ($\mu_{riding} = 31.11$ μg/g Cr, $\mu_{driving} = 30.01$ μg/g Cr, $\mu_{stationary} = 41$ μg/g Cr), DHEA-S ($\mu_{riding} = 107.35$ pg/mL, $\mu_{driving} = 99.71$ pg/mL, $\mu_{stationary} = 90.43$ pg/mL), and the cortisol to DHEA-S ratio ($\mu_{riding} =$

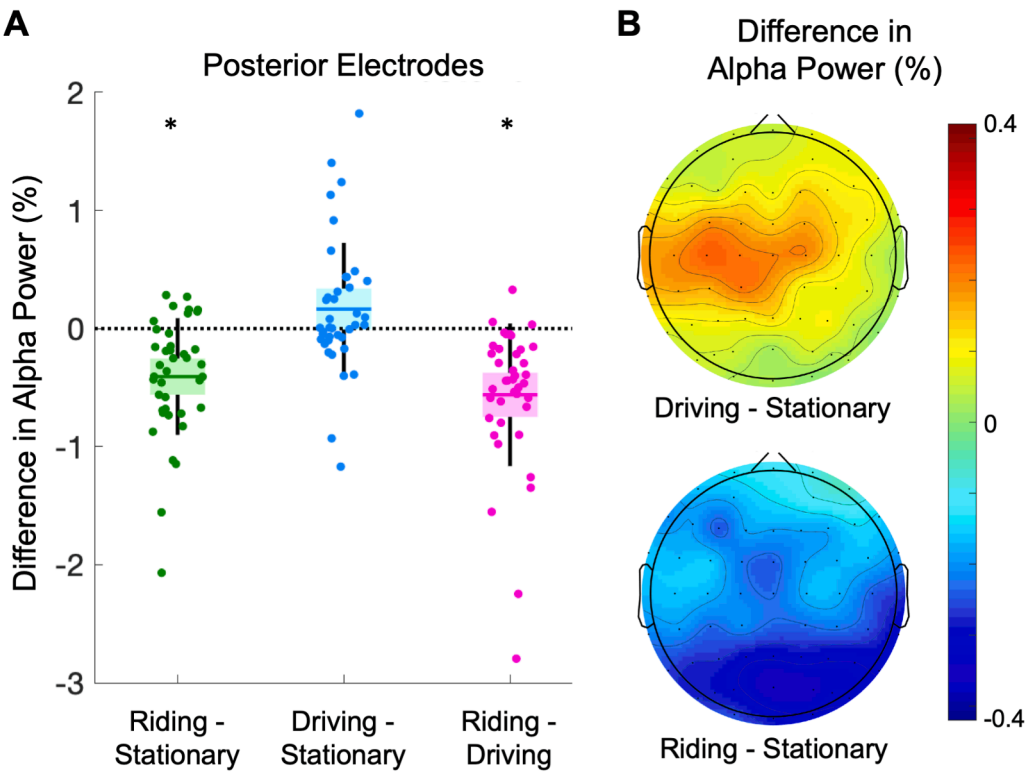

Fig. 2. Relative Alpha Power. A. Relative alpha power was less in the riding condition than in either the stationary or driving conditions. Power was calculated over O1, Oz, O2, PO3, POz, and PO4 from 8 to 12 Hz. The horizontal line, box, error bars, and markers reflect mean, standard error of the mean, standard deviation, and individual points, respectively. Asterisks illustrate $p_{corrected} < 0.05$. B. Topographs of relative alpha power while riding and driving as compared to the stationary condition show a decrease in relative alpha power over parieto-occipital scalp during riding that was not observed during driving, consistent with enhanced visual attention during riding.

12.0, $\mu_{driving} = 12.0$, $\mu_{stationary} = 14.4$).

There was a significant effect of condition on epinephrine concentration ($F(2,82) = 12.07$, $p < 10^{-4}$, Fig. 3B). Epinephrine levels were higher after riding than during the stationary condition ($\mu_{riding\ -\ stationary} = 3.2$ μg/g Cr, $t(41) = 4.6$, $p_{corrected} < 10^{-4}$) and higher after riding than after driving ($\mu_{riding\ -\ driving} = 2.4$ μg/g Cr, $t(41) = 4.0$, $p_{corrected} < 10^{-3}$). Driving did not increase epinephrine relative to the stationary condition ($\mu_{driving\ -\ stationary} = 0.8$ μg/g Cr, $t(42) = 1.21$, $p_{corrected} = 0.24$). There was no correlation between epinephrine and MMN (riding: $r = -0.12$, $p_{corrected} = 0.987$; driving: $r = 0.07$, $p_{corrected} = 0.68$; stationary $r = -0.14$, $p_{corrected} = 1.00$), nor between epinephrine and relative alpha power (riding: $r = 0.07$, $p_{corrected} = 1.00$; driving: $r = 0.13$, $p_{corrected} = 1.00$; stationary $r = 0.02$, $p_{corrected} = 0.89$).

There was an effect of condition on cortisol levels ($F(2,80) = 6.5$, $p < 0.01$). Cortisol levels were lower after riding than the stationary condition ($\mu_{riding\ -\ stationary} = -10.19$, $t(40) = 2.7$, $p_{corrected} < 0.05$) and lower after driving than the stationary condition ($\mu_{driving\ -\ stationary} = -10.98$, $t(41) = 2.8$, $p_{corrected} < 0.05$). Condition had a significant effect on DHEA-S levels ($F(2,88) = 90.43$, $p < 0.01$). DHEA-S levels were higher after riding than the stationary condition ($\mu_{riding\ -\ stationary} = 16.91$, $t(45) = 2.7$, $p_{corrected} < 0.05$) and higher after driving than the stationary condition ($\mu_{driving\ -\ stationary} = 12.87$, $t(44) = 2.7$, $p_{corrected} < 0.05$).

The cortisol to DHEA-S ratio data from the riding condition were not distributed normally (Shapiro-Wilks test, $p < 10^{-6}$); thus, we applied the natural logarithm to all conditions to normalize the distribution before conducting significance tests. Differences here are reported in log space. Condition had a significant effect on the cortisol to DHEA-S ratio ($F(2,80) = 15.7$, $p < 10^{-5}$, Fig. 3C), which was lower after riding than while stationary ($\mu_{riding\ -\ stationary} = -0.18$, $t(41) = 4.48$, $p_{corrected} < 10^{-3}$) and lower after driving than while stationary ($\mu_{driving\ -\ stationary} = -0.19$, $t(41) = 4.74$, $p_{corrected} < 10^{-4}$). Driving and riding did not differ from each other significantly ($\mu_{riding\ -\ driving} = 0.02$, $t(40) = 0.51$, $p_{corrected} = 0.612$). There was no effect of condition on testosterone levels ($F(2,90) = 0.26$, $p = 0.77$, Fig. 3D).

2.4. Self-Report

We collected self-report data on the effect of motorcycling on self-reported perceptions of anxiety and stress from 27 participants. Participants responded 'makes much better' for motorcycling affecting their anxious mood (48%, $p_{corrected} < 10^{-4}$), tension (52%, $p_{corrected} < 10^{-4}$), fears (26%, $p_{corrected} < 0.05$), insomnia (22%, $p_{corrected} < 0.05$), intellect (26%, $p_{corrected} < 0.05$), depressed mood (74%, $p_{corrected} < 10^{-7}$), and stress (78%, $p_{corrected} < 10^{-8}$, Fig. 4). All respondents reported that riding a motorcycle reduced both their depressed mood and stress.

3. Discussion

In this study, we tested the hypotheses that motorcycle riding—an arousing activity—increases both selective attention and sensory monitoring, consistent with riders' self-reports of heightened sensory perception. The results support both hypotheses; in the riding condition (vs. the driving and stationary conditions), we observed a diminished N1 and a decrease in posterior relative alpha power, consistent with, respectively, decreased auditory processing of distracters and enhanced visual processing, that together support increased focus in the visual modality. We also observed an enhanced MMN while riding, consistent with enhanced pre-attentive sensory monitoring. While the changes in epinephrine levels did not correlate with changes in MMN, the mean elevations in heart rate and epinephrine levels during riding suggest a heightened state of arousal while riding. These data provide ecologically-valid support for the hypothesized interaction between arousal and cognitive processing (Sara, 2009; Sara and Bouret, 2012), here applied specifically to selective attention and sensory processing. Finally, the decreased cortisol and cortisol to DHEA-S ratio during riding provide data consistent with the self-reported stress reduction that accompanies the riding experience (Heaney et al., 2013). Similarly, and in various stress reduction activities, cortisol levels were found to be decreased (Miluk-Kolasa et al., 1994; Yount et al., 2013).

It is theoretically possible that the N1 decreased during riding because of increased noise artifacts (e.g., from motion). We believe that

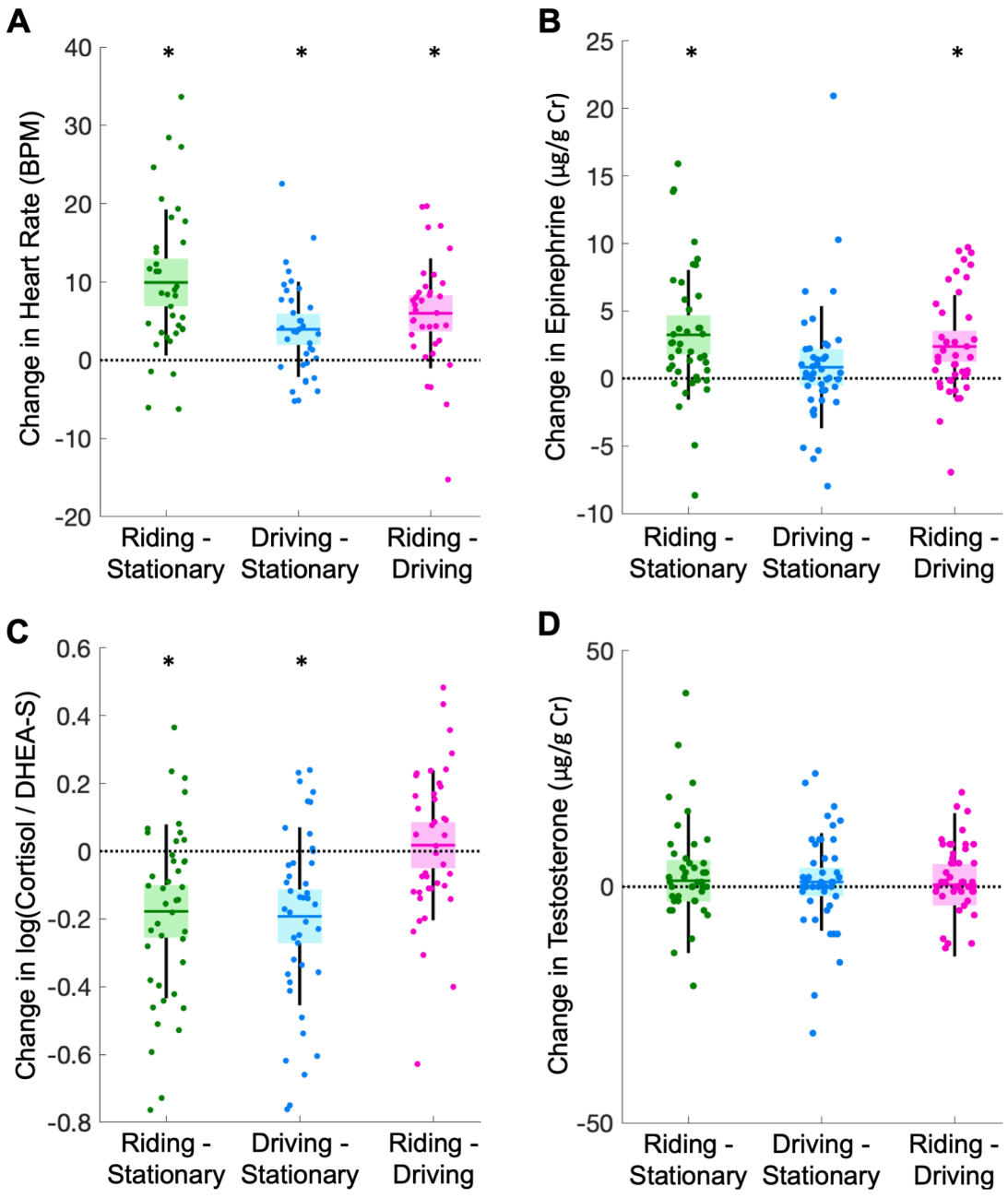

Fig. 3. Heart Rate and Hormones. Change in heart rate and hormone concentration measures between the three experimental conditions. A. Heart rate differed between all conditions. The stationary data were collected before riding or driving. B. The concentration of epinephrine in urine was significantly greater after riding than while stationary or driving. C. The cortisol to DHEA-S ratio was lower while riding and driving than while stationary. D. There was no effect of condition on testosterone levels. The horizontal line, box, error bars, and markers reflect the mean, standard error of the mean, standard deviation, and individual points, respectively. Asterisks illustrate $p_{corrected} < 0.05$.

this is unlikely to explain the entire effect, as we also observed a decrease in posterior relative alpha power during this condition, consistent with enhanced visual attention (Pfurtscheller, 2003; Romei et al., 2008). Further, if noise was a primary determinant of N1 magnitude, then we would expect a bigger effect on (or increase in the variability of) the N1 in the oddball condition, which had considerably fewer trials than the standard condition, but we did not observe this. We therefore find it doubtful that the N1 decrease during riding can be explained by a selective increase in noise.

The second key finding – that the MMN was greater during riding than while stationary – is consistent with the prediction that riding heightens sensory monitoring. This interpretation supports the perspective that the MMN captures processes, such as stimulus anticipation at the level of the auditory cortex (Näätänen et al., 2007), that enable us to switch our attention to an important alternative stimulus (e.g., a siren or horn while riding). This finding also contributes to the debate about whether the MMN is a distinct neural process or an extension of the N1; for reviews, see (Garrido et al., 2009; Näätänen et al., 2007). Given that riding exerted opposite effects on the N1 (decrease) versus on the MMN (increase), selective attention and sensory monitoring seem to be separable neural processes. The interpretation of broad sensory enhancement aligns with research showing an increased MMN response in meditators (Biedermann et al., 2016; Luo et al., 1999; Singh and Telles, 2015; Srinivasan and Baijal, 2007), as well as attenuated MMN amplitude and/or latency in cases of cognitive dysfunction (Ford and Mathalon, 2012; Huttunen-Scott et al., 2008;

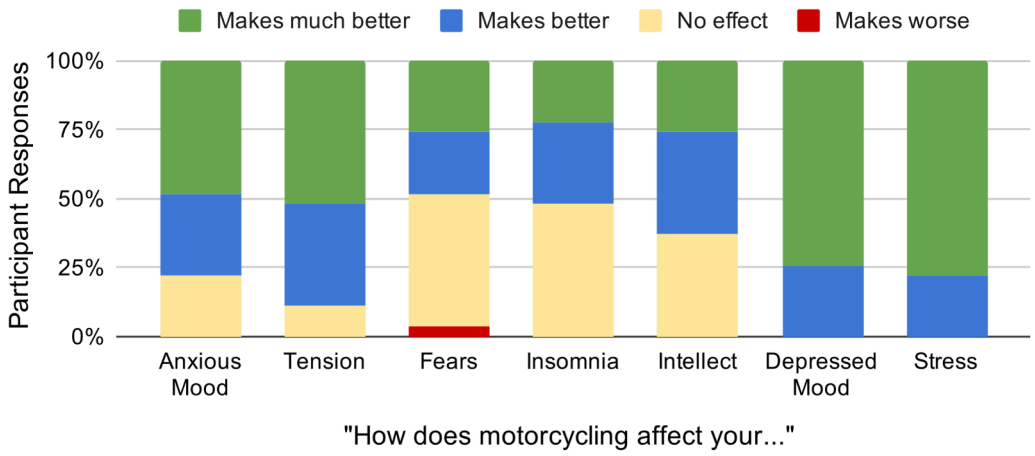

Fig. 4. Modified HAM-A for Motorcycling. Participants reported that riding a motorcycle made better or made much better their anxious mood (78%), tension (89%), fears (48%), insomnia (52%), intellect (63%), depressed mood (100%), and stress (100%). Changes in all seven categories were statistically significant.

Näätänen et al., 2014; Shelley et al., 1991; Umbricht and Krljes, 2005). Together with the effects on N1, these results suggest that riding modifies attentional processes via two mechanisms: tuning selective attention away from auditory distracters and toward visual processing, and heightening the brain's passive monitoring of changes in the sensory environment.

The hormonal data support a comparison of motorcycling with light exercise. Specifically, the observed increase in epinephrine and heart rate suggest that riding significantly activates the SAM system; driving, however only increased heart rate, and to a lesser degree than riding. The magnitude of the increase during riding is commensurate with the magnitude of physiological changes during light exercise (Pearson et al., 1995; Zouhal et al., 2008), even though riding is a seated activity and epinephrine production is known to decrease in the seated position (Christensen and Brandsborg, 1973; Von Euler and Hellner, 1952). Supporting this interpretation, the decrease in posterior alpha band power during periods of silence while riding (relative to while stationary or driving) is similar to the effects of caffeine. Namely, the magnitude of this change in brain activity while riding suggest an increase in alertness, analogous to the boost provided by a cup of coffee (Angelakis et al., 2004; Barry et al., 2005; Dimpfel et al., 1993; Reeves et al., 1995).

Our results support the conclusion that riding results in SAM activation and alterations in the HPA axis. The latter alteration resulted in a decrease in cortisol, an increase in DHEA-S level, and a decrease in the cortisol/DHEA-S ratio. Driving showed similar changes in HPA hormone concentrations. The decrease in cortisol levels could not be related to diurnal variations because the ordering of the conditions was pseudorandomized. Although DHEA-S and cortisol are produced by the adrenal cortex upon HPA activation and the release of adrenocorticotropic hormone from the pituitary, and activation the synthesis of pregnenolone, the first precursor for both synthesis pathways of cortisol and DHEA-S, DHEA-S and cortisol responses are quite different under certain conditions. It has been shown that an imbalance of cortisol/DHEA secretion may occur when an individual experiences chronic stress (Gill et al., 2008) as well as in acute exercise in moderately active and endurance trained groups (Heaney et al., 2013). The latter condition resembles the changes seen in experienced motorcycle riding. However, it may be that the sustained and task-concentrated attention required in riding (and in other rapid and demanding activities such as skydiving, scuba, tennis, etc.) and activities engaged in natural exposure to environment offer a means of stress reduction by drawing the riders' limited attentional resources away from other stressful factors in their lives (e.g., psychosocial concerns) (Ewert and Chang, 2018). This formulation challenges the notion of "stress," as one might suppose that operating a rapidly-moving motorcycle is, on its own, "stressful"—yet, at least among our relatively-experienced group of participants, it did not independently trigger a large physiological stress response. Future studies may choose to assess the temporal nature of this hormonal shift in search of prophylactic potential, given that elevated glucocorticoid levels have been shown to contribute to neuronal death, among other undesirable outcomes (Dinkel et al., 2003; Kerr et al., 1991; Krystal, 1993; Uno et al., 1989).

One limitation of our results is that we collected self-report data significantly after study participation. It is possible therefore, that participants' responses might not exactly reflect what their responses would have been on the day of their participation. However, given that our participants were experienced riders, we believe it likely that participants would be clear on how motorcycling generally affects them, and would give similar answers whether we asked them the day they rode in the experiment or significantly afterwards.

An important observation from the present studies is that advances in technology have made it possible, and even practical, to collect high-quality electrophysiological data in real-world conditions that are remarkably well controlled. With judiciously-selected tasks, such as the auditory oddball task, researchers can collect hundreds of evoked response trials without interfering significantly with the daily activity of operating a motor vehicle. This is of particular relevance to attention research; laboratory conditions can test only a limited range of attention-demanding distractors, whereas the phenomenon of sustained attentional "focus" requires the brain to maintain attention while immersed in numerous environmental distractions. In other words, in a simple split-attention task (e.g., auditory vs. tactile or auditory vs. visual), participants can control attention relatively easily by suppressing the single distracter channel. In real-world conditions however, individuals must sustain their attention even when distractors may arise from any sensory modality. The present study lends ecologically-valid support to existing theories of interactions between arousal and attention, and to the dissociation of selective attention and sensory monitoring as distinct neural processes, while quantifying the holistic experience of riding a motorcycle.

4. Methods and materials

4.1. Participants

We recruited 77 participants (23 females, age 42 ± 14 years) from southern California using an IRB-approved recruitment flyer. The protocol was approved by IntegReview Independent Review Board Services (https://integreview.com/), and all participants provided written informed consent. Participants were required to answer screening questions. Inclusion criteria were as follows: between 18 and 70 years old, neurologically healthy, not taking antipsychotics, and comfortable

riding a motorcycle (on a 5-point scale, we accepted participants who rated their comfort as a 3 or greater; mean score was 4.7). We did not validate the participants' self reports. Following exclusion of data due to noise, artifacts, and acquisition errors, the final sample comprised 42 participants.

4.2. Experimental design and stimuli

In this experiment, participants engaged in three activities (Fig. 5). They rode a motorcycle ("riding") and drove a car ("driving"), and before and after each of these conditions, participants sat in a chair outside, overlooking the road ("stationary"). During each activity, we collected EEG and electrocardiographic (EKG) data while delivering auditory stimuli (following an auditory oddball paradigm, below) via headphones. The auditory oddball paradigm was nested within a 7-minute track that included a 6-minute block of the oddball paradigm and a 1-minute block without tones. The track looped continuously for the entirety of each condition. The block without tones provided a stimulus-free recording to assess power in the alpha (8–12 Hz) band in the EEG signals during driving and riding. In addition, during the stationary condition, participants provided passive drool saliva samples; immediately after the stationary condition, participants gave urine specimens. These measures were used to assess hormonal responses during each activity. When combined with heart rate data extracted from EKG, these data reflect complementary dimensions of physiological arousal. The initial stationary condition and biosample collections gave us a reference point against which to compare the effects of subsequent riding or driving. The stationary condition immediately after riding or driving allowed us to detect whether changes in brain activity persisted after driving and riding ceased. The order of the driving and riding conditions was pseudo-randomized to counterbalance temporal effects. Both riding and driving conditions lasted approximately 22 min, while each stationary condition lasted 7 min. This was a repeated-measures design—all participants engaged in all activities.

4.3. The course

We conducted the experiment at two separate locations: Angeles Crest Highway outside Los Angeles[1] (37 participants) and Mesa Grande at Lake Henshaw[2] (40 participants). Both routes were single-lane roads, were open to the public, and contained no stoplights. We elected to collect data at multiple locations to accommodate facility use constraints and to ensure a diverse group of participants. Both routes took approximately 22 min, round trip, to complete. In the riding condition, participants rode their own motorcycle, whereas in the driving condition, participants drove a provided car (Lexus NX200). We conducted the experiment only during optimal driving conditions: no precipitation, extreme cold, or traffic. There were no meaningful differences between the routes.

4.4. Auditory oddball paradigm

We used the auditory oddball paradigm (Segalowitz and Barnes, 1993) to assess sensory processing during stationary, riding, and driving conditions. In the oddball paradigm, auditory tones were presented to both ears at regular intervals (on average, 1.5 s apart). The paradigm was passive, meaning that no overt response was required of the participants. The tones were presented at both low and high frequencies (500 Hz and 750 Hz) and, critically, the prevalence of the frequencies was unbalanced (77% vs. 23%, respectively). Accordingly, the less-frequent tones are defined as the "oddball" stimuli; the more frequent tones are defined as the "standard" stimuli. These simple auditory tones were generated using pulse width modulation on an Arduino (https://www.arduino.cc/) and delivered via Bose QuietComfort 20 acoustic noise-cancelling headphones to suppress background interference from engine noise. All participants confirmed they were able to hear the tones in all conditions.

This design is validated to elicit an N1 response, a fronto-central negativity around 100 ms post-stimulus onset, that corresponds to the auditory brain response to auditory tones. The oddball tones also elicit a mismatch negativity (MMN) response, a fronto-central negativity with a peak between 100 and 250 ms following stimulus onset, associated with the detection of a change in the auditory background. The MMN typically is expressed as a difference wave (oddball - standard). The design thus measures the auditory brain response to the tones and evaluates pre-attentive sensory processing of the oddball stimuli.

4.5. EEG/EKG recording

During each condition, we sampled and recorded brain activity and heart rate at 500 Hz using a 64-channel EEG cap and 2-channel active EKG from the eego sports package by ANT Neuro (https://www.ant-neuro.com/). The EEG electrodes were sintered Ag/AgCl, with active shielding, and the default reference is CPz – a very stable location for subjects who are in motion. The cap and EKG were connected by custom cables into an amplifier and laptop situated in a backpack worn by users. We asked all participants if there was any discomfort from the equipment: backpack, EEG, earbuds. We adjusted the equipment on the few riders who replied yes until said discomfort was relieved, before allowing them to participate.

4.6. EEG preprocessing and analysis

All processing of the EEG data was performed in MATLAB (v. R2018b, Mathworks Inc.) using EEGLAB software (v.14.1.2) (Delorme and Makeig, 2004). All subjects' data were processed as follows: EEG data were down-sampled to 250 Hz and trimmed to remove any pre- or post-recording signals, dominated by task-unrelated noise. A high-pass filter (0.75 Hz) was applied to remove artifacts due to slow drifts. We then used the Artifact Subspace Reconstruction (ASR) algorithm (Chang et al., 2018), first to identify and then to remove bad channels, as well as to remove extreme artifacts in the data. Our criteria dictated that channels should be removed if they (i) contained more than 15 min of flat line data or (ii) failed to meet a correlational threshold (specifically, correlation >0.7 with other channels for a majority of the data). The ASR algorithm first constructs a subspace representation of artifact-free data as a reference and then uses this reference to identify windows along the time series that depart from this subspace statistically, indicating the presence of artifact; these windows are then reconstructed based on the clean data. The key parameter in this approach is the definition of artifact, which we based on the number of standard deviations by which a window deviated from the reference data. Based on a formal assessment (Chang et al., 2018), we adopted a threshold of 100 standard deviations, which provides a very conservative approach that identifies only the most extreme artifacts. Critically, because this algorithm operates within a moving window (1–2 s in width) along the time series, it is capable of identifying non-stationary, extreme artifacts that are not removed easily by any other traditional approach. Thus, we used the ASR algorithm to eliminate large transient artifacts (like motion, which we expect from motorcycle riding) while preserving the data. The technique was developed for real-time, brain-computer interface applications, making it well-suited to our experiment. The cleaned data were re-referenced to the average reference. Following the removal of gross transient artifacts, we used independent component analysis (Extended Infomax Algorithm) (Lee et al., 1999; Makeig et al., 1996) to identify remaining artifacts that were more stationary: (i) eye blinks and lateral movements, (ii) pulsations, and (iii) any remaining channel deviations.

From the cleaned data, we extracted features of interest. We

[1] 34°16′09.0″N 118°08′46.6″W.
[2] 33°13′54.1″N 116°45′33.2″W.

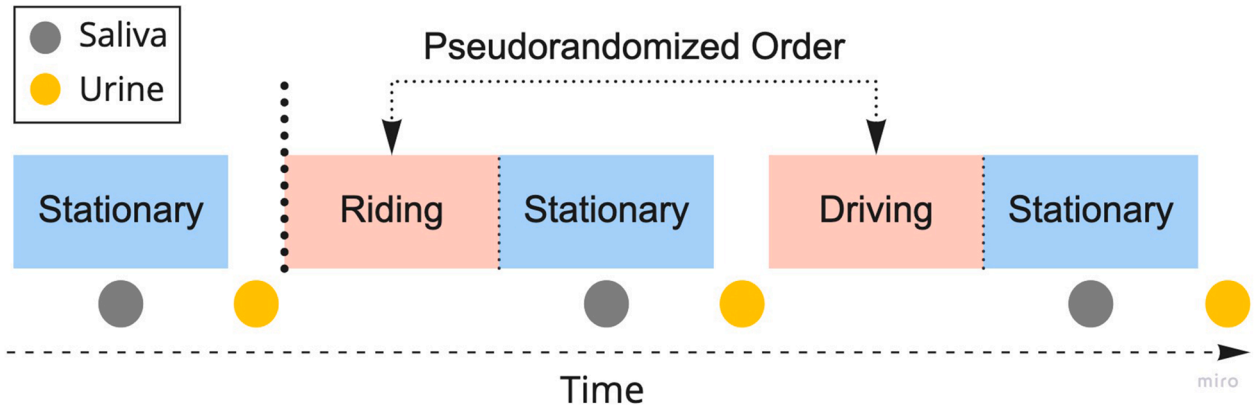

Fig. 5. Experimental Design. Participants rode a motorcycle ("riding") and drove a car ("driving"). Before and after each of these conditions, participants sat in a chair outside, overlooking the road ("stationary"). We recorded EEG and EKG during all of these conditions. During the stationary condition, participants gave passive drool saliva samples; immediately afterward, participants gave urine specimens. All participants engaged in all conditions and sample collections.

quantified N1 and MMN at electrode Fz, consistent with prior reports (Näätänen et al., 2007; Näätänen and Picton, 1987), though we note that the topography of these effects has a broad fronto-central distribution (Fig. 1B/D). The N1 was calculated by extracting 1-second epochs extending from −100 ms to 900 ms following each auditory stimulus. We averaged epochs separately for oddball and standard auditory tones. Mean baseline voltage (−100 to 0 ms) was subtracted from each average ERP. The latency of the N1 peak at electrode Fz was identified as the minimum in the 50–150 ms window following onset of the stimulus. For the MMN peak latency at Fz, we first calculated the difference wave, subtracting the standard ERP from the oddball ERP, and then identified the minimum in the 100–250 ms window following onset of the stimulus. For both the N1 and MMN, we averaged data in a 10 ms window around the peak to increase the signal to noise ratio.

We calculated spectral features, namely alpha power, by applying the fast fourier transform (as implemented in EEGLAB's std_spec.m), to the concatenation of all one-minute periods of no tones. This concatenation led to an average no-tone sample length of 3 min. Specifically, we calculated *relative* alpha power: absolute alpha power (8–12 Hz) divided by absolute full spectrum power (0.75–30 Hz). Each of these two values were obtained by averaging power values from the following posterior electrodes: O1, Oz, O2, PO3, POz, and PO4. This was motivated by known, *a priori* posterior distribution of modulation effects in the alpha frequency range during visual attention (Foxe and Snyder, 2011; Romei et al., 2010; Silva et al., 1977).

4.7. EKG preprocessing

Raw EKG signals were bandpassed between 0.5 Hz and 50 Hz, and QRS complexes were extracted using MATLAB peak detection to infer heart rate. The average timing of these events across a condition constituted the heart rate, which we report in beats per minute (BPM).

4.8. Hormone measurement

We elected to collect hormone measurements using salivary and urinary methods, to avoid the stress response from multiple blood draws. We forbade participants from eating during the experiment. Participants were allowed to drink one small bottle of water throughout the entire experiment, but not before saliva collection periods. ZRT Laboratory (https://www.zrtlab.com/) provided the collection materials and processed all samples. Specific protocol details are in Supplementary Online Materials.

We used liquid chromatography with tandem mass spectrometry (LC-MS/MS) on saliva and dried urine samples to assay hormone levels (ZRT Labs, https://www.zrtlab.com/). Testosterone, and DHEA-S concentrations were gathered from saliva.

4.9. Self-Report

Several months after collecting the EEG, hormone, and heart rate data (mean 22 months), we sent participants an online, modified version of the Hamilton Anxiety Rating Scale (HAM-A) to quantify the subjective effect of motorcycle riding on metrics of anxiety and stress (Hamilton, 1959). Specifically, we asked how motorcycling affected the first 6 items in the HAM-A (anxious mood, tension, fears, insomnia, intellect, and depressed mood) as well as stress. For example: "How does motorcycling affect your depressed mood?". Participants answered on a 5 point likert scale from "makes much worse" to "makes much better". Question order was randomized for each participant.

4.10. Statistical methods

We analyzed EEG event-related potential responses under the general linear model. We tested all hypotheses using a one-factor, repeated-measures ANOVA with condition (riding, driving, stationary) as the within-subject factor. We list degrees of freedom as $F(df_{condition}, df_{error})$. $df_{condition}$ is $k-1$, where k is the number of conditions and df_{error} is $(n-1) * (k-1)$, where n is the number of participants. For results that differed significantly from chance, we conducted post-hoc, paired, two-tailed, t-tests.

Non-normally-distributed heart rate data and cortisol to DHEA-S ratio, as assessed by the Shapiro-Wilks test, were transformed using the natural logarithm before employing statistical testing. Effect size and significance were computed by mean. Missing samples were excluded rather than imputed, and thus, the degrees of freedom varied slightly between tests. We corrected all t-tests for multiple comparisons, shown as $p_{corrected}$, using the Holm-Bonferroni procedure (Holm, 1979). HAM-A data were assessed for statistical relevance using a paired *t*-test, where we considered 'makes much better' to be value 1, no change as 0, and 'make worse' as −1.

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Credit authorship contribution statement

Don A. Vaughn: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft. **Michael B. Maggiora:** Investigation, Project

administration, Resources, Software, Supervision. **Kathryn J. Vaughn:** Project administration, Resources, Supervision. **Christina J. Maggiora:** Project administration, Resources, Supervision. **Amir-Vala Tavakoli:** Investigation. **William Liang:** Investigation. **David Zava:** Resources. **Mark S. Cohen:** Conceptualization, Investigation, Methodology, Resources, Supervision, Writing - original draft. **Agatha Lenartowicz:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - original draft.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brainres.2020.147203.

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