Low alcohol doses reduce common 10-15 Hz input to bilateral leg muscles during quiet standing

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Abstract

The effects of low doses of alcohol on neural synchronization in muscular activity were investigated in ten participants during quiet standing with eyes open or closed. We focused on changes in common input to bilateral motor unit pools as evident in surface EMG recordings of lower leg extensor and flexor muscles. The extensor muscles exhibited bilateral synchronization in two distinct frequency bands, i.e., 0-5 and 10-15 Hz, whereas synchronization between flexor muscles was minimal. As expected, alcohol ingestion affected postural sway yielding increased sway at higher blood-alcohol levels. Whereas vision only affected bilateral synchronization at 0-5 Hz, alcohol ingestion resulted in a progressive decrease of synchronization at 10-15 Hz between the EMG activities of the extensor muscles. The decrease in common bilateral input is most likely related to reduced reticulospinal activity with alcohol ingestion.

Keywords: MU synchronization, posturography, ethanol, physiological tremor, common drive
Introduction

Synchronization is a significant feature of neural activity underlying motor control. Neural activity, as measured using encephalography (EEG and MEG) and electromyography (EMG), displays oscillations in distinct frequency bands, indicating local synchronization of small neural clusters. Spatially distributed neural structures can also synchronize and the level of both types of synchronization can be affected differentially by various task variables. For instance, during static contraction EMG activity is coherent with EEG and MEG activity recorded above the contralateral motor cortex in the beta band, i.e., 15-30 Hz (e.g., Conway et al. 1995; Kilner et al. 2000; Salenius et al. 1997). Similarly, coherent activity has been measured between EMGs of different muscles (Farmer et al. 1993; Kilner et al. 1999). The task-related modulation of synchronization provides a window into the functional interactions during motor control and suggests a functional role of neural synchronization (Farmer 1998; Grosse et al. 2002; Salenius and Hari 2003).

A currently thriving method to explore the underlying mechanisms and function of neural synchronization is to probe the neural dynamics by changing relevant organismic and task constraints, for instance, by administering pharmacological agents (Baker and Baker 2003; Jensen et al. 2005; Riddle et al. 2004). Although the disruptive effects of alcohol on behavior are well understood for years (e.g., Carpenter 1962; Koelega 1995), alcohol has seldom been used to probe neural synchronization. Laboratory studies of acute alcohol effects in social drinkers have indicated that alcohol disrupts performance in a wide range of activities (for a review, see Fillmore 2003) and alcohol intoxication has long been associated with deteriorated motor control, in particular postural control during upright standing (Nieschalk et al. 1999; Noda et al. 2004; Woollacott 1983). Given the robust effects of alcohol intake on postural control, it may be expected that it also affects the underlying neural synchronization.
In the present study, we investigated the acute effects of alcohol intake on bilateral motor unit (MU) synchronization\(^1\) during quiet standing. In previous studies, we found an increase of 10 Hz synchronization between bilateral MU pools during fatiguing contractions of homologous leg (Boonstra et al. 2007b) and upper arm muscles (Boonstra et al. 2007a), reflecting increased common input at 10 Hz (cf. Christou et al. 2007). Evidence for common input in this frequency range has also been found on a behavioral level, where bilateral movement discontinuities at 8-10 Hz are coupled for in-phase but not for anti-phase finger movements (Evans and Baker 2003). Such changes in bilateral coupling reveal functional connectivity that may be brought about by different neural pathways mediating bilateral interactions (Carson 2005). Alcohol-induced changes in bilateral common input might further elucidate the possible neural mechanisms underlying bilateral synchronization at 10 Hz. If bilateral synchronization results from a common supraspinal input, it may be expected to decrease with alcohol ingestion concomitant with a decline in postural balance. The effect of low alcohol doses on bilateral MU synchronization in lower leg muscles was tested by means of the standard Romberg test to differentiate between different sources of postural imbalance (e.g., through differential effect of visual information).

Methods

Participants

Ten healthy male students (age 19-23 years; weight 70-80 kg) volunteered to participate in the experiment. Participants were instructed to have a decent meal prior to the experiment, which took place between 12:00 and 15:00 hrs. All participants gave their informed consent

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\(^1\) MU synchronization is a term that has traditionally been used to specifically reflect the correlated discharge of action potentials between pairs of motor units examined in the time domain (see, e.g., Harrison et al. 1991). More recently, different forms for MU synchronization have been reported that may reflect different underlying neural mechanisms. Here, we use the term MU synchronization to refer to all forms of synchronized activity of either pairs of MUs or MU pools.
after the experimental procedure and all accompanying instructions had been explained to them in detail. The experiment was carried out in full compliance with the Helsinki Declaration and was endorsed by the ethics committee of the Faculty of Human Movement Sciences, VU University Amsterdam, before its conductance.

Procedure
The experiment included four blocks of quiet standing trials, each consisting of one eyes-open (EO) and one eyes-closed (EC) trial. Trial duration was 45 seconds. The order of the trials in each block was randomized. The first block was a baseline assessment in which participants were sober. The subsequent blocks, lasting 20 minutes each, started with consuming a shot of alcohol (vodka containing 37.5% alcohol) dissolved in orange juice (shot1: 30 ml vodka and 30 ml orange juice; shot2: 40 ml vodka and 40 ml orange juice; shot3: 50 ml vodka and 50 ml orange juice). The total amount of consumed alcohol was 0.51 and 0.45 g/kg for participants of 70 and 80 kg, respectively. After each alcohol consumption participants waited approximately 15 minutes before performing two quiet standing trials. The blood alcohol concentration (BAC in ‰) was determined 20 minutes after each alcohol consumption using a digital breath analyzer (ACE-3000, ACE GmbH, Simbach am Inn, Germany).

Data acquisition
Participants were asked to stand barefoot on a force platform (9281B, Kistler, Reeuwijk, The Netherlands). The feet were placed 8 cm apart and arms were hanging relaxed alongside the body. Force signals were sampled at 100 Hz and converted to center-of-pressure (COP) time series (8-channel charge amplifier, 9865E, Kistler, Reeuwijk, The Netherlands). Surface EMG was recorded bilaterally from three ankle plantar flexion or extensor muscles, i.e., lateral gastrocnemius (GL), medial gastrocnemius (GM) and soleus (SO), and two ankle dorsiflexion or flexor muscles, i.e., tibialis anterior (TA) and extensor digitorum longus (ED), in the lower legs. Electrodes were placed in a bipolar configuration with an inter-electrode distance of about 2 cm. EMG data were amplified, on-line band-pass filtered (10-1000 Hz),
and stored on a disk with a sampling frequency of 2 kHz (Porti 5-16/ASD, TMS International, Enschede, The Netherlands).

Data analysis

**COP time series:** The COP represents the point of application of the ground reaction force on the force platform and reflects the orientations and movements of bodily segments aimed to keep the center of gravity over the base of support. Postural steadiness was quantified using two commonly used posturographic measures derived from the acquired COP time series, i.e., sway amplitude and sway area. To this end, the mean and linear trend were subtracted from mediolateral and anterioposterior COP trajectories, which transformed the original time series into \( x \) and \( y \) time series, respectively. Subsequently, \( x \) and \( y \) time series were bi-directionally filtered (second-order low-pass Butterworth filter, cut-off at 12.5 Hz) and the resultant distance time series \( r(t) \) was constructed using \( r(t) = \sqrt{x(t)^2 + y(t)^2} \) (Prieto et al. 1996), with \( t = 1, 2, 3, \ldots, T \) with \( T \) indicating the total number of analyzed samples in the COP time series (i.e., 4500 samples). The sway amplitude was defined as the average distance of the mean-centered posturogram to the origin and determined by taking the mean of \( r(t) \) (i.e. in mm; see Prieto et al. 1996, eq. 4). Second, the area of postural sway was defined as the area covered by the ellipse enclosing approximately 95% of the samples along the COP trajectory and was determined using \( F \) statistics assuming that the distances \( x(t) \) and \( y(t) \) were normally distributed (i.e. in mm\(^2\); see Prieto et al. 1996, eq. 18).

**EMG time series:** Surface EMG data were filtered off-line using a second-order bi-directional high-pass Butterworth filter (cut-off at 20 Hz) to eliminate possible movement artifacts (Hayes 1960). Subsequently, the EMG signals were full-wave rectified by determining their Hilbert amplitude (cf. Journee 1983; Journee and van Manen 1983; Myers et al. 2003). The amplitude of surface EMG reflects net MU activity, that is, the recruitment and the discharge
rates of the active MUs, and can therefore be regarded as an index of the level of activation provided by the spinal cord (Farina et al. 2004). Coherence between EMG amplitudes recorded above different muscles can then be used to quantify common synchronized input to both MU pools. Bilateral coherence between EMG activities of homologous muscles was estimated using Welch’s periodogram method with Hamming windows of 2048 samples length and 1024 samples overlap, resulting in a frequency resolution of 0.98 Hz (Welch 1967). Note that coherence analysis between surface EMGs differs from both cross-correlation (Harrison et al. 1991) and common drive analysis (Mochizuki et al. 2006) of intramuscular recordings in that it quantifies the extent to which input to different MU pools is synchronized at a certain frequency (cf. Boonstra et al. 2007b; Farmer 1999; Sowman et al. 2006).

...insert Figure 1 about here...

Statistics

To test whether coherence was significantly different from zero, the 95% confidence interval was determined for individual coherence spectra (Amjad et al. 1997). Assuming independent Gaussian processes, the 95% confidence interval can be determined by \(1/(0.05)^{(1/(L-1))}\) with \(L\) representing the number of disjoint segments used for the coherence estimate. Because we employed overlapping instead of disjoint segments, we adjusted the confidence interval using the correction factor for overlapping windows (Welch 1967). Based on the resulting coherence spectra (Fig. 1), two frequency bands were discerned: a lower (0-5 Hz) and a higher (10-15 Hz) frequency band. Fisher’s transform was applied to the coherence spectra to ‘stabilize’ the variances of the underlying distribution (Amjad et al. 1997) and averaged over each frequency band before testing for significant differences across conditions.

A repeated-measures analysis of variance (ANOVA) was conducted on all dependent variables with the within-subject factors alcohol (4 levels: baseline, shot1, shot2, shot3) and
vision (2 levels: EO and EC). Effect sizes for main and interaction effects are reported as partial eta squared values ($\eta^2_p$).

Results

**BAC:** A one-way repeated measures ANOVA indicated that BAC changed significantly with the factor alcohol ($F_{(3,27)} = 105.6, P < 0.001, \eta^2_p = 0.92$). With alcohol intake, BAC increased significantly (shot1: 0±0‰, shot2: 0.27±0.04‰, shot3: 0.57±0.05‰; ± denotes standard error). BAC was always 0‰ at the baseline assessment.

**Sway amplitude and sway area:** Significant main effects of alcohol and vision were observed for sway amplitude and area (Table 1). Both followed a biphasic pattern, that is, postural sway reduced after the first shot of alcohol and then increased with shot2 and shot3 to values above baseline (Fig. 2). Post hoc paired-samples $t$-tests revealed that the effect of alcohol was mainly due to increased sway amplitude in the shot3 condition, i.e., there was a significant increase from baseline to shot3 ($t_{(9)} = -2.99, P = 0.015$), from shot1 to shot3 ($t_{(9)} = -3.34, P = 0.009$), and from shot2 to shot3 ($t_{(9)} = -2.46, P = 0.036$). Post hoc analyses of the effect of alcohol ingestion on sway area revealed a similar trend (see also Fig. 2), although the respective increments failed to reach significance ($P = 0.057, 0.051$ and $0.073$, respectively). Sway amplitude and sway area were significantly larger for standing with eyes closed (4.05±0.27 mm and 189±31 mm$^2$, respectively) than for standing with eyes open (3.44±0.23 mm and 131±18 mm$^2$, respectively). There were no significant interaction effects (Table 1).

...insert Table 1 and Figure 2 about here...

**Coherence between homologous muscles:** Coherence spectra revealed a different pattern for bilateral flexor and extensor muscles. Whereas coherence was largely absent between flexors, two frequency bands were clearly discernable in the coherence spectra of the extensors, i.e.,
0-5 and 10-15 Hz (Fig. 1). The coherence was generally much stronger in the lower than in the higher frequency band. In the lower frequency band at least nine participants showed significant coherence between each extensor pair and five participants for each flexor pair, whereas in the higher frequency band at least six participants showed significant coherence between extensor muscles and three participants between flexor muscles. Alcohol intake had no significant effect on coherence in the lower frequency band (0-5 Hz), whereas in the higher frequency band (10-15 Hz) coherence decreased significantly between bilateral GM and SO muscles (Table 2 and Fig. 3). Alcohol had no significant effect on the coherence between homologous flexors.

With eye closure, a significant increase in coherence between homologous extensors occurred in both frequency bands, apart from the coherence between SO muscles in the higher frequency band, which was not significant but followed a similar trend \( P = 0.086 \). In the lower frequency band, coherence increased in the EC condition compared to the EO condition with 0.054±0.012, 0.044±0.012, and 0.028±0.010 for GL, GM, and SO, respectively. In the higher frequency band, the increment in coherence with eye closure was 0.018±0.009, 0.022±0.007, and 0.022±0.012 for GL, GM, and SO, respectively. For the flexors, coherence in the lower frequency band increased significantly with eye closure only for TA muscles (increment, 0.011±0.004). Significant interaction effects were absent (Table 2).

Discussion

According to the results of the Romberg test, alcohol ingestion resulted in an increase in sway amplitude and sway area. In line with the findings of Nieschalk and colleagues (1999), the amount of sway tended to decrease after the first shot to then increase again to levels above baseline (Fig. 2). Sway amplitude and sway area increased when participants closed their
eyes, but no interaction with alcohol was found, indicating that the effects of alcohol on postural control were independent of the availability of visual information (cf. Kubo et al. 1989; Nieschalk et al. 1999; Uimonen et al. 1994). This may suggest that the neural site affected by alcohol is located in the central vestibular system or perhaps mainly in the (vestibulo-)cerebellum (cf. Diener et al. 1983). In support, several studies indicated that alcohol strongly disrupts or interferes normal cerebellar functioning (e.g., Carta et al. 2004; Carta et al. 2006; Hanchar et al. 2005). In chronic alcoholics, for example, brain damage was observed in the form of grey and white matter loss in the cerebellum (Harper 1998), while the amount of sway has been selectively related to the volume of the cerebellar vermis (Sullivan et al. 2006).

Bilateral coherence between homologous muscles revealed MU synchronization between extensor muscles in two frequency bands, 0-5 and 10-15 Hz (see Fig. 1). Synchronization in the lower frequency band is most likely related to co-modulation of muscle activation (Mochizuki et al. 2006; Saffer et al. 2007). We found that bilateral synchronization between 0-5 Hz was higher in the EC condition matching the increase in sway amplitude and area (cf. Saffer et al. 2007). This stands in contrast to the studies of Mochizuki and colleagues who reported that the common drive to individual MUs of bilateral SO muscles did not differ between standing with eyes open and eyes closed (Mochizuki et al. 2007; 2005), which could be attributed to differences in the methods that were employed to estimate bilateral synchronization. Coherence between rectified surface EMG, as used here, quantifies the common input to bilateral MU pools (see Methods), whereas the common drive analysis used by Mochizuki and colleagues quantifies the common input to individual MUs (Mochizuki et al. 2005). Common input to individual MUs is thought to be mainly caused by last-order branched presynaptic fibers and presynaptic synchronization (Gibbs et al. 1995). In contrast, synchronization between surface EMGs (or the net activity of two MU pools) does not require that spike trains of individual MUs of both MU pools coincide (Elble and Randall 1976). Hence, while individual MUs may not receive more common input, bilateral muscles may still be activated in a more synchronous manner due to more pronounced sway with eyes
closed, causing the here-reported increase in bilateral synchronization between 0-5 Hz (cf. Saffer et al. 2007, for a similar interpretation).

Bilateral synchronization in the 10-15 Hz frequency band followed a different pattern: not only was it higher in the EC condition but, unlike 0-5 Hz synchronization, it also progressively decreased with alcohol intake. The different effects of alcohol and vision on MU synchronization in both frequency bands point at different underlying mechanisms. Bilateral synchronization at 10-15 Hz found in the present study was in all likelihood related to the 10 Hz oscillations that are ubiquitous in motor-related neural activity. In view of their diversity in the face of variations in organismic and task conditions, the 10 Hz oscillations appear to be multi-factorial in origin (McAuley and Marsden 2000). These oscillations are particularly apparent in physiological tremor and during slow finger movements (Farmer 1999). Although tremor activity is generally uncoupled between bilateral limbs (Lauk et al. 1999; Marsden et al. 1969), bilateral MU activity can couple weakly around 10 Hz under specific circumstances, such as during fatiguing bilateral contractions (Boonstra et al. 2007a; Boonstra et al. 2007b). Similarly, the 10-Hz discontinuities, as observed during slow finger movements (Vallbo and Wessberg 1993), were bilaterally synchronized for in-phase but not for anti-phase movements of both index fingers (Evans and Baker 2003). Therefore the here-reported effects on bilateral synchronization at 10-15 Hz seem to reflect changes in neural interactions leading to synchronized input to bilateral MU pools. In accordance to a previous study (Boonstra et al. 2007a), common input around 10 Hz was mainly found between homologous extensor muscles, while synchronization between flexor muscles was largely absent.

The increase in bilateral 10-15 Hz synchronization in the EC condition seems to be in accordance with increased 10 Hz activity at higher levels of muscle activation (Boonstra et al. 2007b; Christou et al. 2007; Ebenbichler et al. 2000). That is, the larger sway in the EC condition was accompanied by increased muscle activation and might thus also be related to the increased synchronization at 10-15 Hz. The exact origin of increased 10 Hz activity with muscle activation is an issue of ongoing debate (e.g., Erimaki and Christakos 2008), but it is
unlikely that it is caused by a direct cortical drive at 10 Hz, as corticospinal synchronization is generally absent or weak around 10 Hz. Instead, there might be an indirect link between the increase in descending input and increased spinal oscillations at 10 Hz, for instance by affecting a mechanism that prevents MUs from synchronizing to descending input at 10 Hz (Baker et al. 2003).

However, bilateral 10-15 Hz synchronization and sway did not reveal the same pattern in relation to alcohol ingestion, excluding an obvious link between bilateral MU synchronization and postural sway. The effect of alcohol on neural functioning is widespread, but two effects seem particularly relevant in relation to the decrease in bilateral synchronization. First, alcohol reduces the effectiveness of various reflex pathways (Davidoff 1973; von Dincklage et al. 2007; Woollacott 1983) and reflex loops play a significant role in the generation or modulation of 10 Hz oscillations (Lippold 1970). A reduced stretch reflex might thus diminish the 10 Hz oscillations similar to the effect of anesthetics (Sowman et al. 2006). Although reduced 10 Hz activity does not directly explain reduced bilateral synchronization, some spinal cord interneurons communicate between the two sides of the cord (Bajwa et al. 1992; Dietz and Berger 1982) and may cause a concomitant reduction in bilateral coupling. Second, alcohol may affect central oscillators that either project bilaterally or are bilaterally coupled. Several structures with strong connections with the cerebellum could produce synchronous input to bilateral MU pools, such as vestibulospinal tract neurons that project bilaterally (Kandel et al. 1991; Shinoda et al. 1986). The cerebellum has generally been related to different tremors (Deuschl et al. 2001) and, as explained above, cerebellar activity is strongly affected by alcohol. Hence, reduced cerebellar activity with alcohol ingestion might thus result in reduced bilateral synchronization at 10-15 Hz. In support, Grosse and Brown (2003) demonstrated that the normal acoustic startle reflex was associated with an increased bilateral synchronization between 10-20 Hz, which they associated with increased reticulospinal activity. Similarly, other studies have attributed unilateral 10-20 Hz activity in the leg muscles to supraspinal drive (Hansen et al. 2005), and vestibulospinal drive in particular (Dakin et al. 2007).
Hence, while spinal involvement cannot be fully excluded, it seems likely that the reduction in bilateral common input at 10-15 Hz with alcohol ingestion can be attributed to reduced reticulospinal activity. As such, EMG-EMG coherence, in particular between bilateral EMG activities, may provide a valuable addition to the more established technique of EMG-EEG and EMG-MEG coherence. In general, corticospinal synchronization has been found mainly in the beta band (see Introduction) and related to the corticospinal drive. Coherence between bilateral EMGs seems to be sensitive to other descending motor pathways, such as the reticulospinal system, that may not be accessible using corticospinal coherence analysis (cf. Grosse and Brown 2003, for a similar conclusion). Indeed, preliminary results from our group reveal bilateral EMG synchronization around 10 Hz that is not present in the coherence spectra between EMG and contra-lateral EEG activity (B.C.M van Wijk et al., unpublished observation).
Grants

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References


Legends

**Figure 1.** Mean coherence spectra for EC trials at baseline (black) and after three shots of alcohol (grey). The coherence between bilateral extensor muscles (i.e., GL, GM, SO) decreased with alcohol intake in the in the higher frequency band (10-15 Hz). The coherence between bilateral flexor muscles (i.e., TA and ED) was generally much lower. Dashed lines represent the 95% confidence interval (see Methods).

**Figure 2.** Main effects of alcohol (baseline, shot1, shot2, shot3) on sway amplitude (left panel) and sway area (right panel). Error bars represent the standard error.

**Figure 3.** Main effects of alcohol (baseline, shot1, shot2, shot3) on the coherence between homologous extensors (left panels) and flexors (right panels) in the lower (0-5 Hz, upper panels) and higher (10-15 Hz, lower panels) frequency bands. Error bars represent the standard error.

**Table 1.** Main and interaction effects of the within-subjects factors alcohol (4 levels: baseline, shot1, shot2, shot3) and vision (2 levels: EO, EC) on sway amplitude and sway area.

**Table 2.** Main and interaction effects of the within-subjects factors alcohol (4 levels: baseline, shot1, shot2, shot3) and vision (2 levels: EO, EC) on the coherence between homologous extensor and flexor muscles in the lower (0-5 Hz) and higher (10-15 Hz) frequency bands.
The graphs depict the sway amplitude and area across different conditions.

**Sway Amplitude**
- **Baseline**
- **Shot 1**
- **Shot 2**
- **Shot 3**

**Sway Area**
- **Baseline**
- **Shot 1**
- **Shot 2**
- **Shot 3**
**extensors**

Coherence [0–5 Hz]

Coherence [10–15 Hz]

**flexors**

Coherence [0–5 Hz]

Coherence [10–15 Hz]
Table 2. Results ANOVA of bilateral EMG synchronization

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<th>Vision</th>
<th>Interaction</th>
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<td>ED</td>
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*ns not significant

*In case the assumption of sphericity was violated, the number of degrees of freedom was adjusted using the Huynh-Feldt method (corrected degrees of freedom are not listed here)
Table 1. Results ANOVA of behavioural data

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ns not significant

*a In case the assumption of sphericity was violated, the number of degrees of freedom was adjusted using the Huynh-Feldt method (corrected degrees of freedom are not listed here)