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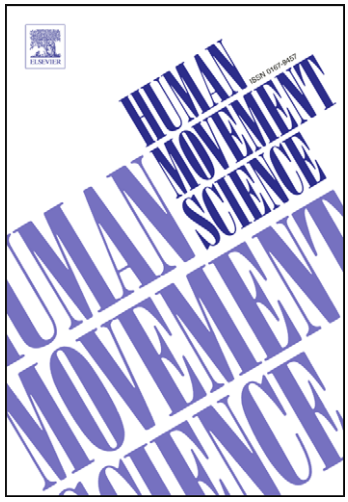

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Running head: SPONTANEOUS BLINKS ARE ENTRAINED BY TAPPING

Spontaneous eye blinks are entrained by finger tapping

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Abstract

We studied the mutual cross-talk between spontaneous eye blinks and continuous, self-paced unimanual and bimanual tapping. Both types of motor activities were analyzed with regard to their time-structure in synchronization-continuation tapping tasks which involved different task instructions, namely "standard" finger tapping (Experiment 1), "strong" tapping (Experiment 2) requiring more forceful finger movements, and "impulse-like" tapping (Experiment 3) where upward-downward finger movements had to be very fast. In a further control condition (Experiment 4), tapping was omitted altogether. The results revealed a prominent entrainment of spontaneous blink behavior by the manual tapping, with bimanual tapping being more effective than unimanual tapping, and with the "strong" and "impulse-like" tapping showing the largest effects on blink timing. Conversely, we found no significant effects of the tapping on the timing of the eye blinks across all experiments. The findings suggest a functional overlap of the motor control structures responsible for voluntary, rhythmic finger movements and eye blinking behavior.

Keywords: Spontaneous Endogenous Blinks, Unimanual and Bimanual Finger Tapping,

PsycINFO classification: 2300 Human Experimental Psychology; 2330 Motor Processes.

Spontaneous eye blinks are entrained by finger tapping

1. Introduction

Humans are well equipped with different adaptive mechanisms, which have evolved to guarantee successful and optimal behavior in changing habitat conditions. Eyeblink behavior is an example of such optimized behavior. Blinking is so effortless that usually individuals do not pay attention to it: blink execution does not require much cognitive effort. However, blinking behavior is not as simple. There are different types of eyeblinks which serve to distinct functions: (i) spontaneous or involuntary blinking serves the physiological needs of the ocular system; it avoids eye-drying as it spreads tears on the surface of the cornea and conjunctiva (e.g., McEwen, 1962; Stern, Walrath, & Goldstein, 1984). (ii) Voluntary blinking (Gittins, Martin, Sheldrick, Reddy, & Thean, 1999) is self-initiated or due to the request of an experimenter in response to an external stimulus; it has been studied in relation to visual functions (Volkmann, Rigs, Ellicott, & Moore, 1982). (iii) Reflexive blinks (e.g., Esteban, 1999; Pellegrini, Horn, & Evinger, 1995) are involved in the startle reflex (Filion, Dawson, & Schell, 1998) and play indirect defensive as well as protective roles. The latter occur in response to various stimuli which mirror potentially dangerous situations for the eyes; they result from different types of eyeblink reflexes such as air-puff-, acoustic-click-, or dazzling-light-induced reflex blinking. The present study focuses on the spontaneous blinks registered in parallel to finger tapping movements in different experimental conditions. The conditions for the eyes were kept constant to avoid any threat stimuli, which could elicit a reflexive eyeblink.

The physiological basis of blinking is simple: two antagonistic muscles, the *levator palpebrae superioris* and *orbicularis oculi*, participate in eyelid movements during blinking (Evinger, Manning, & Sibony, 1991; Esteban, Traba, & Prieto, 2004); turning off the otherwise

tonically active *levator palpebrae superioris* together with bursts of activity of the *orbicularis oculi* causes a rapid lowering of the upper eyelid. The opposite process elevates the eyelid back to the upper position (Evinger, 1995). Recently, it has been established that there is a distributed brain network active during blinking: the primary motor cortex, the supplementary motor area, the cingulate motor cortex, the dorsolateral prefrontal cortex, the posterior parietal cortex, the visual cortex, the central thalamus, and the cerebellum participate in spontaneous as well as in voluntary and reflexive blinking (Tsubota, Kwong, Lee, Nakamura, & Cheng, 1999).

The functional role of spontaneous blinking is mainly to guarantee protection against corneal drying (Evinger, et al. 2002) which is avoided by an appropriate tear film distribution over its surface (Evinger, 1995; VanderWerf, Reits, Smit, & Metselaar, 2007). While reduced blinking leads to tear film thinning, longer prevention of blinks can eventually result in the tear film breaking up (Holly, 1973). Due to altered blink rates observed in “dry eye” cases (e.g., in the video display terminal syndrome (Tsubota, Hata, Okusawa, Egami, Ohtsuki, & Nakamori, 1996)), a blepharospasm, i.e., an abnormal, involuntary blinking or spasm of the eyelids (Hallett, 2002), is quite frequent today as the visual information intake from printed materials and electronic displays, e.g., computer, television, mobile devices increases rapidly. Reports of spontaneous blink rates differ, ranging from 12/min (King & Michels, 1957) up to 24/min (Collins, Seeto, Campbell, & Ross, 1989). Individuals with a spontaneous blink rate greater than 20 blinks/min constitute a “frequent eyeblink activity” group (Doughty & Naase, 2006). All these reported rates are much higher than required to keep the cornea moist (Evinger, 1995), which indicates the involvement of the blink mechanism in various processes different from motor control.

In general, a task requiring visual vigilance and attention reduces the blink rate (Bauer, Strock, Goldstein, Stern, & Walrath, 1985), whereas intensified sympathetic stimulation increases it. Therefore, the importance of studying the blink rate is widely acknowledged not only from theoretical but also from practical and clinical points of view. Blinking behavior was found to be influenced by various external factors (Ponder & Kennedy, 1927): blink rate (and blink amplitude) dramatically changes with the psychological and perceptual factors such as attention, stress, fatigue, emotional, or other cognitive states. Therefore, spontaneous blinks can be good markers of completion of cognitive tasks such as a solution of arithmetic problems (e.g., Evinger, 1995). It was also found that blinking often accompanies other tasks with some regularity, for instance, at “physical gaps”, “punctuation-marks” during reading, or at the onset of redirecting the gaze when sequentially looking at multiple objects (Hall, 1945). Eyeblinks can also be related to selective attention, and they can also serve as an indicator to disclose deception (Fukuda, 2001).

These factors mostly reflect cognitive (cortical) aspects, i.e., the central stage of blink control. Analysis of blink rate and interblink-interval distributions revealed different types of blink patterns (Zaman & Doughty, 1997; Doughty, 2001). Doughty (2001) promoted the idea that blinks are controlled by a central pacemaker, which resides in the basal ganglia. Freudenthaler, Heuf, Kadner, and Schlote (2003) provided further support to this view. Observing the various blink patterns during video display terminal usage, they presumed that at least the frequency of homogenous blink patterns can be based on the endogenous pacemaker. However, heterogeneous patterns could also originate from a central pacemaker if it is assumed that blink behavior is modulated by both internal and external factors. Further evidence for the idea of central or endogenous control is derived from the dopamine hypothesis of blink control

which assumes that blink rate is a neurobiological measure of dopaminergic activity (Dreisbach, et al. 2005; Taylor, et al. 1999; cf., van der Post, de Waal, de Kam, Cohen, & van Gerven, 2004). The supposed linkage between dopaminergic activity and spontaneous blinks is in agreement with clinical studies of psychiatric and neurological patients suffering from the consequences of an altered dopaminergic activity such as in Parkinson disease, schizophrenia, depression, etc. (MacLean, et al. 1985; Bodfish, Powell, Golden, & Lewis, 1995).

Beside these central factors involved in blink control, an essential role of peripheral factors has also been acknowledged, e.g., a damage of an ocular surface (Tsubota, et al. 1996), an ocular anaesthesia (Naase, Doughty, & Button, 2005), a presentation of sensory stimuli to eye surface (Nakamori, Odawara, Nakajima, Mizutani, & Tsubota, 1997), and effects due to pharmacological substances (Dudinski, Finnin, & Reed, 1983). Thus, a controversy about the dominance of central vs. peripheral factors of blink control has evolved. However, a combined hypothesis has also emerged; it emphasizes primacy of the central control being potentially modulated by the peripheral factors (Naase, Doughty, & Button, 2005). Following this line of thought, one can assume that if exogenous blink-generating stimuli are eliminated (e.g., as a result of anaesthesia or in constant environmental conditions), then the central control should define the blink behavior. Furthermore, if the central blink generator with a stationary pace rate is in operation, then the generator will determine the intervals between blinks, though the intervals will still show some random fluctuations (Ponder & Kennedy, 1927; Naase, et al. 2005).

This study primarily addresses the central pacing mechanism of spontaneous blink generation. Its operation in the autonomous pacing mode was shown to be limited by psychological factors as discussed before. However, it is not yet clear from current literature

whether *repetitive* motor actions have different modulatory effects on blinking. To be more specific, one can ask: how does the repetition of a simple voluntary motor action (which is based on an internal clock) influence spontaneous blinking? Addressing this question, our study investigated spontaneous blinking behavior during voluntary repetitive finger tapping, a motor task which has been widely used in a number of investigations to examine issues of motor and perceptual timing as well as other effects such as task concurrency and laterality of neuropsychological functions.

The finger tapping task as designed by Stevens (1886) includes two subsequent phases (Fig. 1A). In the synchronization phase, participants tap in synchrony with an external pacer. In the following continuation phase, they tap maintaining the target rate without the external pacing using their own internal pacer (Further details of this paradigm are described in the Section "Procedure"). Various control mechanisms of tapping were proposed from a motor timing perspective, such as a single central pacemaker which successively provides relevant intervals and triggers motor commands each time an interval has elapsed (Wing, 2002).

There is consistent evidence from recent studies that, due to the open loop situation, self-paced tapping in the continuation phase is highly sensitive to interferences with other ongoing processes. Notably, the temporal accuracy of periodic tapping with the dominant hand has been found to suffer from the concurrent execution of another (discrete) motor task with the non-dominant hand (Yoshino, Takagi, Nomura, Sato, & Tonoike, 2002; Wachter, Cong, Staude, & Wolf, 2008). The opposite effect, i.e., an influence of tapping on a concurrent motor task, is also documented in our earlier studies (Wachter, Cong, Staude, & Wolf, 2008). These findings are of particular interest for the present investigation which studied the interaction between continuous

and spontaneous motor tasks, since they suggest that eye blinking may affect manual tapping as well.

Thus, analyzing blinking behavior during the execution of a tapping task should provide further indications about whether blinking and finger tapping share some central control mechanism. If this is not the case, spontaneous blinking should be independent of concurrently active repetitive motor processes, indicating that the implementations of multiple concurrent central commands for blinks and finger movements are not constrained by a common bottleneck. To address these issues, four experiments, each with different tapping demands were conducted in which blink patterns and tapping behavior were monitored. Compared to normal "standard" tapping (Exp. 1), "strong tapping" (Exp. 2) required more pronounced force generation leading to a greater finger movement amplitude, whereas "impulse-like tapping" (Exp. 3) stressed a very fast execution of movements. In the fourth (reference) experiment, tapping was omitted. We anticipated that more arduous conditions could lead to a stronger interaction between the tasks.

2. Methods

2.1 Participants

Seven (two female, five male) right-handed healthy participants (P1-P7) took part in this investigation. They had neither signs nor a history of neurological disorders or motor diseases. They all volunteered to participate in the study and gave their informed consent according to the International Ethical Guidelines for Biomedical Research (2002).

Fig. 1 about here

2.2. Experimental setup

Participants were seated with elbows comfortably semi-flexed, their forearms and palms rested on a table (ulnar side down), which allowed the effortless bimanual tapping with the index fingers. Moving the fingertip up and down with the upper position being the resting position they performed tapping. Two force transducers were embedded in the tabletop for recording the finger taps (ground contact of the index finger tips of both hands). Two high-resolution laser distance sensors (LAM50-10, WAYCON, Germany) fixed about 10 cm above the table surface registered the actual vertical position of fingers. A single-channel high-gain differential input electrooculogram amplifier module (EOG100B, Biopac Inc., USA) was used together with two Ag-AgCl electrodes placed above and below the right eye referenced to linked mastoids (as used e.g., by Skotte, Noygaard, Jorgensen, Christensen, & Sjogaard, 2007) for tracking the eyeblinks. An ADC (PCI-6025E, National Instruments Inc., USA) digitized all signals at a sampling rate of 1 kHz, and data were stored on a computer. The experiment was controlled by DIAdem (National Instruments Inc., USA) software. Sample traces are shown in Fig. 2.

Fig. 2 about here

2.3 Procedure

An experimental session consisted of 25 trial blocks. As shown in Fig. 1A, each trial started with a synchronization phase, where a sequence of five acoustic pacing signals (duration 50 ms, 500 Hz tone, sound level 79 dB, silence noise level was 40 dB) with an interstimulus interval (ISI) of 550 ms was presented to participants to synchronize their periodic finger tapping. Participants were instructed to proceed with tapping in a self-paced mode at the same rate after pace ceased in the subsequent so-called continuation phase. However, different from the original Stevens's (1886) concept, the continuation phase of each trial was additionally

divided into 12 (bi-partite) segments: the first part of each segment (with duration randomly selected between 6 s and 8 s) involved pure self-paced tapping, whereas in the second resynchronization part, an additional triad of pacing signals helped to stabilize the tap rate in self-pacing. The onset of the first pace within the triad was synchronized with the actual tap, whereas the next two paces occurred with an ISI of 550 ms as in the synchronization phase. Short pauses of 8 s (which could be extended by the participants by pressing a footswitch) were interspersed between the 25 trials. The first trial of the experimental session served for some tapping practice and was omitted from the data evaluation. Total time during which of blinks were collected and assessed was about 25 minutes for each condition; this is far beyond the minimum standard recording period of five minutes which was proved to be sufficient for spontaneous blinking analysis (Zaman & Doughty, 1997). Diurnal variations of blink rate (Barbato et al., 2000) were minimized as the four experiments of each individual were conducted at the same daytime, mostly in the morning and later afternoon hours.

2. 4 Tapping experiments and conditions

Each experiment was split into two parts. The first 13 trials were dedicated to unimanual tapping with the index finger of the dominant hand only, followed by 12 trials of bimanual tapping with both index fingers simultaneously. Two participants performed in reverse order but no order effect was found. In the unimanual condition, the non-dominant (inactive) index finger rested on the force sensor surface. All seven participants took part in all four experimental conditions.

Experiment 1: standard tapping. The participants could tap as they felt comfortable, without any specific instruction about finger movement and contact force.

Experiment 2: strong tapping. The participants received instructions to tap stronger, i.e., with a force more pronounced than in the case of standard tapping but not exaggerated (to avoid fatigue).

Experiment 3: impulse-like tapping. The finger tap had to be as short lasting as possible. A specific instruction was given: the upward and downward movements of the finger tip had to be as fast as possible and the duration of ground contact had to be as short as possible. No tap force restrictions were applied.

Experiment 4 (reference): no tapping at all. To obtain patterns of the interblink interval distribution at rest, the participants were exposed to the same experimental setup but without performing a manual task.

Sample records of taps as performed in these different experiments are shown in Fig. 3; they clearly demonstrate the different movement profiles for each condition.

Fig. 3 about here

2.5 Data analysis

Data evaluation was based on custom-made scripts for MATLAB (MathWorks, Inc.). The main task was the detection of all motor events in the raw data as shown in Fig. 2. Onsets of taps were automatically determined in the force as well as in the position signals (Hofer, et al. 2005); subsequently, an experimenter visually evaluated detection accuracy and, if necessary, interactively corrected event detections.

The following events were specifically defined when a blink was detected:

The finger tap occurring before the blink onset represents the *reference tap* (reference event) and defines the time origin (i.e., $t = 0$) within this segment (see Figs. 1B and 4).

The onset time t_b of the blink event relative to the reference tap was normalized by the ISI and expressed as phase $\Phi = t_b / \text{ISI}$.

The phase Φ describes the instant of the blink within the actual cycle of the periodic tapping, with $\Phi = 0$ (as well as $\Phi = 1$ due to periodicity) indicating simultaneous (in-phase) execution of a blink and a tap, and $\Phi = 0.5$ indicating that a blink occurred in the middle of a periodic tapping cycle. Based on reference taps and blink phases, phase resetting curves and phase histograms were computed for each tapping experiment in order to assess possible mutual interactions between spontaneous blinking and tapping.

Fig. 4 about here

2.6 Phase resetting curves

In order to investigate the mutual effects of spontaneous blinking and periodic tapping, we used the *phase resetting curve* method (Fig. 4) introduced by Yoshino et al. (2002); basically, the resetting curve depicts the timing of the periodic taps around the blinks as a function of the blink phase Φ within the periodic tapping process. For each blink, the last preceding periodic tap was designated as the *reference tap* (labelled as R in Fig. 4); for timing analysis, the intertap intervals (ITIs) were assessed: two intervals preceding the reference tap (unaffected due to causality) together with three intervals following the reference tap (maybe affected by the blink), contained in a tap group of six taps for each blink. Each tap is indicated by a symbol. The vertical distance between the symbols (star, circle, and triangle) represents the ITI as shown in Fig. 4A. Together all of these tap groups build the phase resetting curve: (i) vertically, they are aligned such that the reference tap is located at t = 0 of the ordinate (showing the ITIs), and (ii) horizontally, they are placed at their phase value Φ which results from t_b being the time interval between the reference tap and the blink. The time of the blink occurrences is indicated by the inclined dashed

line. - What is expressed by the phase resetting curve? (i) If the blink occurrence is independent of the periodic tapping, the tap groups are uniformly distributed over phase Φ, and (ii) if the periodic tapping process is not affected by the blinks, taps (represented by dots) form equidistant horizontal dot lines only, as shown in Fig. 4B. Any systematic deviation from this undisturbed tapping after the reference tap, however, would indicate a mutual influence of the blinks and the periodic tapping process. For illustration, Fig. 4C depicts the case where the blink event completely restarts the periodic tap cycle, thus the distance between the inclined dashed line and the dot line above it is equal to the ITI (i.e., discrete action affects the periodic action). In contrast, the dots in Fig. 4D are restricted to small phase values Φ, indicating that the blink execution becomes synchronized with the periodic tapping (i.e., periodic action affects the discrete action).

2.7 Distribution of blink phases

If the interblink intervals are described by a stochastic process (Hoshino, 1996; Greene, 1986) and if both processes, tapping and blinking are progressing independently of each other, the observed phases Φ describing their temporal relationship should show a uniform distribution of their values within [0, 1[. However, if there is some systematic interaction between the blink and tapping process, the histogram of the observed blink phases Φ should be shaped. Thus, any deviation of the phase histogram from the expected uniform distribution would indicate an influence of the tapping process on the blink behavior.

Since both the phase resetting curve and the phase histogram are constructed with the phase values $\Phi = t_b$ / ISI (i.e., based upon ISI), ideally, they require the participants to perfectly reproduce the pacing frequency, i.e., equalize ITI with ISI. For real data, however, the measured ITI is scattered around the ISI value. Therefore, the measured quantities will slightly differ from

their ideal theoretical expectations, even when the blink and tapping processes are completely independent. For instance, a blink occurring at the end of an actual ITI (which is longer than the targeted ISI) may result in a phase value $\Phi > 1$, which is not compatible with the strictly cyclic interpretation allowing phase values $0 \leq \Phi < 1$ only. In order to assess the effects of scattered ITI on the phase histogram and phase resetting curve, for each participant, the blink series of the reference experiment was combined with the tapping series of the corresponding session of Experiment 1. Then, we evaluated each phase as described above for this new (artificial) signal combination. This new set combines two definitely uncorrelated signals since they were recorded in different experiments but it still comprises the effects of scattered ITI. Thus, a phase resetting curve and phase histogram of this dataset serves as a reference for independent processes in real measurements.

3. Results

Mean contact forces (in N) and mean contact durations (in ms) generated by the participants in all three tapping experiments are summarized in Table 1. Consistently for all participants and for both unimanual and bimanual tapping experiments, the mean contact forces were largest in Experiment 2 (“strong“ tapping) whereas mean contact durations were shortest in Experiment 3 (“impulse-like” tapping). This indicates that all participants were capable of adequately performing the required tasks. The longest contact durations obtained in Experiment 2 show that, in general, longer contact durations accompanied the required larger peak force.

Fig. 5 depicts phase resetting curve and phase histogram (normalized by the total number of blinks) of the uncorrelated reference dataset of a typical participant (participant P1). Since the measured ITIs are scattered around the true ISI of 550 ms, dots form clouds instead of the ideally expected horizontal lines (Fig. 5A). Both diagrams are consistent with the theoretical expectation

for independent processes showing a horizontal dot pattern in the phase resetting curve (Fig. 5A) and an approximately uniform distribution in the phase histogram (Fig. 5B), respectively.

Fig. 5 about here

Fig. 6 displays the phase resetting curves of all participants for the three bimanual tapping experiments. All diagrams show that, similar to the phase resetting curves of the (uncorrelated) reference data (Fig. 5A), the six dot-lines are basically horizontal, in particular, the upper three dot-lines of the phase resetting curves stay horizontal. This is a first important finding indicating that the tapping process is not significantly disturbed by the preceding spontaneous blinking.

A second central finding of this study results from the distribution of the dot symbols over phase. Fig. 6 demonstrates that the dots in most cases are not uniformly distributed over phase as in the reference experiment in Fig. 5A, but show a higher density at small phase values. As explicated previously, presence of preferred phases indicates that the periodic taps entrained the onsets of the eyeblinks. The phase resetting curves of the unimanual tapping experiments revealed a similar horizontal orientation of dot-lines but with less pronounced concentration of density at preferred phases. Differences between unimanual and bimanual conditions are elaborated in more detail below.

Fig. 6 about here

The tendency of the participants to execute blinks at preferred phases of tapping is even more obvious in the histograms of the blink phases shown in Fig. 7. Although with different degrees of modulation, all histograms of the bimanual tapping experiments show peaky distributions, which clearly differ from the approximate uniform distributions of the corresponding uncorrelated reference data. The peaks in the distributions obtained from participants P1-P7 (Fig. 7) are located at different phase values indicating some individual

internal delays (typical for each participant). Also, the strength of interference varied between individuals: P1, P4, and P5 showed a very strong effect of tapping upon spontaneous blinking in all experiments, whereas P7 had a less pronounced shaping of phase distributions for standard (uninstructed) tapping, possibly due to the participant's very light surface contact forces.

Table 1 and Fig. 7 about here

Generally, the prominent phase preference was more pronounced in the bimanual tapping experiments than in the unimanual tapping experiments. Fig. 8 demonstrates this difference between unimanual (Fig. 8A) and bimanual (Fig. 8B) tapping for participant P1; this behavior was also typical for the other participants P2-P7.

Fig. 8 about here

For a quantitative analysis, the variable *phase* was tested for deviations from the uniform distribution by performing 2I-tests (Sachs, 1984) separately for each experiment and each individual. The test asserts the null hypothesis that the distribution of the data is uniform; the decision is taken at the significance level $p < 0.05$. In order to prohibit false positive decisions due to scattered ITI, the test was confined to phase values $0 \leq \Phi < 0.8$. Table 2 presents 2I-test values for all participants, conditions and experiments with larger values indicating larger deviations from the uniform distribution. Shaded cells mark 2I values which did not reach significance, while non-shaded cells indicate significant deviations from a uniform distribution. The test expectedly proved the uniform distribution for the reference data (blinking only), consistently showing small 2I values below the significance limit. In contrast, for 38 out of 42 phase distributions obtained in the experiments with tapping the results of the 2I-test indicated significant deviations from the uniform distribution. While the four distributions for which the null hypothesis was not rejected were all obtained in the standard (uninstructed) tapping situation

(Experiment 1), both the strong tapping (Experiment 2) and impulse-like tapping (Experiment 3) data exhibited the non-uniform distributions in all participants. Moreover, with the exception of participant P7, who generally showed a less pronounced shaping of phase distributions in uninstructed tapping (cf., Fig. 7), 2I values were consistently larger in bimanual tapping as compared to unimanual tapping experiments. Thus, the concurrent tapping leads to a stronger entrainment of spontaneous blinking in case of the tapping task (i) being intensified by instruction, or (ii) being performed bimanually.

Table 2 about here

Finally, it should be noted that the modification of Steven's (1886) original tapping paradigm by introducing the re-synchronizing pace triads did not affect the basic finding that the tapping entrains blinking - this was checked in additional pilot experiments without resynchronization. The additional pacing signals reduced the ITI variation to some degree, but it could not preclude the commonly observed tendency to accelerate during self-paced tapping. Such drifts in the continuation phase would hamper the clarity of results since phase is dependent on ITIs. Further, the mean values of the three ITIs before, including and after the blink (see Fig. 1B) were 522.37 ms (SD ± 34.00), 525.59 ms (SD ± 34.50) and 521.36 ms (SD ± 35.50), respectively; thus it is a clear indication that the blink events (occurring after the reference event) did not influence the global timing of the tapping.

4. Discussion

In this study, we monitored blinking behavior in experiments with and without concurrent tapping. Distinct rhythmic finger tapping tasks such as "standard tapping", "strong tapping" and "impulse-like tapping" were applied. The obtained results revealed that self-paced finger tapping at a predefined rate affects spontaneous blinking, whereas the tapping behavior was largely

unaffected by the eyeblinks. This supports the hypothesis that the blinking behavior reflects not only psychological and perceptual factors (such as attention, stress, fatigue, etc.), but also concurrently active simple motor processes. The assumption of a Poisson distribution of the interblink intervals theoretically predicts uniform distributions in phase histograms as shown in Fig. 8 (column 1). The 2I-test, however, rejected the null hypothesis of uniform distribution over phase for the overwhelming majority of tapping data, strongly indicating that blinking in these conditions cannot be considered as being purely spontaneous but rather dependent on the tapping process.

4.1 Brain areas related to finger tapping

Many tapping studies provided evidence for the involvement of multiple brain areas. The results of a meta-analysis of 38 articles (Witt, Laird, & Mayerand, 2008) revealed that primary sensorimotor cortices, supplementary motor area, premotor cortex, inferior parietal cortices, basal ganglia, and anterior cerebellum take part in finger tapping tasks. Moreover, during unpaced continuous tapping neuronal activation increased bilaterally in supplementary motor areas and in the basal ganglia in comparison to (paced) synchronization tapping (Lewis, Wing, Pope, Praamstra, & Miall, 2004). The supplementary motor area participates in many endogenously generated movements and is a prominent candidate for the implementation of an internal clock (Halsband, Ito, Tanji, & Freund, 1993). Thus, it is likely that the supplementary motor area participates in auditory-paced finger tapping (Rao, et al. 1997; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000).

4.2 Brain areas related to blinking

The central control of blinks is based on cortex, extrapyramidal motor tracts and rostral brainstem circuits (reviewed in van Eimeren, et al. 2001). More specifically, blinking activated the supplementary motor area and the right motor cortex along with premotor cortex, basal, ganglia, cerebellum, insula, and midbrain areas. It is important to note that, in comparison to externally induced blinks, increased activation of rostral supplementary motor area and dorsolateral prefrontal cortex was found for endogenous blinks, similarly to hand motor actions (Jenkins, et al. 2000).

Anatomical studies evidenced substantial involvement of cingulate motor areas in upper facial movement: via the efferents of the dorsal and intermediate facial subnuclei, the cingulate area controls the orbicularis oculi and frontalis (Morecraft, Louie, Herrick, & Stilwell-Morecraft, 2001). In primates, the supplementary motor area also sends projections to the medial facial subnuclei which control auricular muscles (Morecraft, et al. 2001). Further, increased activity was reported between the supplementary and cingulated motor areas in spontaneous blinking study of humans (Yoon, Chung, Song, & Park, 2005). Anterior cingulate cortex participates in complex motor behavior (Paus, 2001) and plays some role in bimanual movement coordination (Swinnen & Wenderoth, 2004). Cingulate activity was also found in volitional suppression of blinking (Chung, Yoon, Song, & Park, 2006). In summary, there is compelling neuroscientific evidence that the blinking and bimanual tapping tasks may activate overlapping medial frontal structures (Hanakawa, Dimyan, & Hallet, 2008).

4. 3 Blinking and other motor tasks

So far, the relationship between blinking behavior and other centrally controlled motor monotonous actions (e.g., like gait and respiration) has not been systematically investigated

(Wilson, Fullenkamp, & Davis, 1994). Only speech was considered as an influencing motor action in this regard, and an increased blink rate was observed during verbal tasks (e.g., von Cramon & Schuri, 1980). This is in line with the results of the present study showing a 30 percent average increase of blink rate during tapping as compared to the reference experiment (i.e., without performing a cyclic motor task). Speech combines cognitive and motor functions; however, it is more likely that interference between speech and blinking is due to motor circuits while, in primary motor cortex, eyelid representation neighbours the ones of the tongue, larynx and face (de Jong & Merckelbach, 1990). Thus, the spreading of neural activity ("motor overflow") in these adjacent structures (van Eimeren, et al. 2001; Hanakawa, Parikh, Bruno, & Hallett, 2005) can be partially responsible for the increased blink rate during verbalization.

The present study did not involve verbalization but participation of a subvocal activity (i.e., rehearsal) cannot be excluded; participants could use a rehearsal strategy to optimise their tapping performance. The subvocal activity (i.e., rehearsal) itself could increase a spontaneous blinking rate (von Cramon & Schuri, 1980; de Jong & Merckelbach, 1990) as verbalization related muscles are also active during rehearsal (McGuigan, 1979). However, more recent studies do not support the "motor overflow" based explanation of the interaction (e.g., Morecraft, et al. 2001), acknowledging that the speech and eyelid motor systems share the secondary areas and not the primary motor circuits.

4.4 Tapping and blinking

On the other hand, it is conceivable that the representation of time for speech generation might be derived from an endogenous timing process (or a pacemaker) linked to some type of counting device (Ivry & Richardson, 2002). In line with this assumption, counting out loud from 1 to 100 significantly increased blinking, whereas reciting the alphabet had no significant effects

on blinking (von Cramon & Schuri, 1980). This demonstrates that time-structured simple motor tasks like in our study can be coupled or decoupled from blinking, depending on the task requirements. One can speculate that brain regions engaged in endogenous timing are shared between tapping and blinking tasks; one possible well-suited candidate can be a supplementary motor area (Rao, et al. 1997; Jenkins, et al. 2000).

Concurrent speech and finger tapping studies have documented verbal-manual interactions implying common timing processes (Klapp, 1981; Franz, Zelaznik, & Smith, 1992). Based on the Wing and Kristofferson (1973) model, these earlier studies provided support that the central timing mechanisms are shared across effectors, especially, across such effectors as limb and oral motor systems (Franz, et al. 1992). More recent findings also favoured the notion of a central effector-independent network involved in internal motor timing (Bengtsson, Ehrsson, Forssberg, & Ullen, 2005; Studenka & Zelaznik, 2008), suggesting brain regions such as the supplementary motor area and the superior temporal and inferior frontal cortices as important structures for movement-independent voluntary timing (Bengtsson, et al. 2005; Ullen, 2007). Furthermore, an increased activation was found in the supplementary and cingulate motor cortices, along with sensorimotor areas, putamen and globus pallidus, for internally paced bimanual tapping (Debaere, Wenderoth, Sumaert, Van Hecke, & Swinnen, 2003; Ullen, Forssberg, & Ehrsson, 2003). Patient studies (Ivry & Hazeltine 1999; Kennerley, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002) have demonstrated the importance of subcortical structures for in-phase activation of homologous muscles during bimanual tapping.

Our bimanual experiments, especially the instruction-guided tapping such as the strong and the impulse-like tapping, physically require a higher force and rate of movement, respectively. Thus, increased neural activity is expected in the aforementioned brain regions, along with

stronger triggering of motor commands and higher attentive loads (Johansen-Berg & Matthews, 2002). Indeed, this kind of tapping showed a stronger coupling (phase synchronization caused by phase entrainment) than uninstructed unimanual tapping. In support of these results, Zijdewind, van Duinen, Zielman, and Lorist (2006) found that instructed force production also requires cognitive resources. Further, the existence of a central bottleneck, resonant properties of eyelid motor system, and a widely distributed eyelid-related brain network can create appropriate conditions for the hand motor system to entrain the onsets of concurrent spontaneous movements (blinks) with the onset of its motor events.

Ivry and Richardson (2002) suggested that motor commands for bimanual tapping coming from two hemispheres are integrated for the control of the coordinated behavior. The eyelid movements are generated and controlled centrally, but they are also influenced via certain “secondary paths” (Ponder & Kennedy, 1927). On the other hand, the neural pathways responsible for tapping may cross talk to these “secondary paths” leading to the entrainment of blinks. A major role in these processes can also be assigned to dopaminergic regulation of motor actions (e.g., Dreisbach, et al. 2005). Thus, blinking behavior may indicate the "strength" of the internal representations of motor commands, not only through changes of the blink rate but also through specific timing. Accordingly, the obvious entrainment effect of the strong tapping and impulse-like tapping on blink timing can be due to probably more pronounced motor commands in these cases. Also, the stronger entrainment effect observed in bimanual tapping as compared to unimanual tapping can be interpreted in the same way.

It should be noted that the present findings do not necessarily mean that the tapping task itself directly modulates the spontaneous blinking behavior; alternatively, an indirect influence via a shared central clock can be considered: Actually, it is more likely that tapping affects the

common timing mechanism(s) which also defines the temporal pattern of blink generation. Therefore, any other direct impact on this common timing mechanism can change both the tapping behavior and the blink behavior. Our experiments focus on spontaneous blink behavior; therefore, other parameters were kept constant and only the tapping was manipulated by instruction. However, whether a direct exogenous manipulation of the blink behavior (e.g., startle, air puff, etc.) would influence the tapping behavior, in turn, is a different interesting hypothesis for future research.

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Table 1

Mean contact forces (F) in N and mean contact durations (D) in ms and respective standard deviations (SD) of the right finger tap in unimanual and bimanual tapping conditions. The pooled results of all 7 participants are presented.

	Unimanual				Bimanual			
	F	SD (F)	D	SD (D)	F	SD (F)	D	SD (D)
Exp. 1	1.33	0.47	152.43	40.22	1.10	0.55	128.71	20.55
Exp. 2	5.16	2.20	188.57	45.84	5.13	1.62	191.43	49.27
Exp. 3	1.06	0.30	57.71	17.81	1.02	0.46	53.43	21.33

Table 2

2I-test assertion of the null hypothesis of "uniform phase distribution", shown for all participants and all tapping experiments. Larger values of the 2I-test statistic indicate stronger deviations from the uniform distribution whereas the shaded values mark non-significant differences ($p = 0.05$). The 2I-test indicated significant deviations for the majority of the tapping experiments. Consistently, the expected uniform distribution was confirmed for the reference experiments in all participants.

		Unimanual			Bimanual		
	Ref.	Exp. 1	Exp. 2	Exp. 3	Exp. 1	Exp. 2	Exp. 3
P1	21.54	36.55	29.64	63.20	69.34	95.05	101.78
P2	12.87	29.45	38.16	135.15	98.97	85.77	168.51
P3	18.06	20.09	32.15	168.53	44.19	32.66	172.75
P4	17.83	40.59	38.34	50.00	84.20	126.83	94.49
P5	10.85	96.78	115.64	143.67	218.70	329.14	328.74
P6	15.17	14.51	29.16	32.71	35.28	34.29	81.10
P7	14.27	17.70	39.01	47.34	15.73	54.22	44.55

Figure Captions

Fig. 1. (A) Time course of the tapping paradigm. The basic element is a trial comprising of a synchronization and continuation phase. The latter is divided into 12 segments (6-8 s of duration), each ending with a resynchronization phase (the group of three vertical arrows indicate the three pace signals). The pacing rate, i.e., the interstimulus interval (ISI = 550 ms) was kept constant across all experiments. This paradigm was applied for unimanual and bimanual tapping. (B) Blinks occurring during tapping (zoomed). The interval t_b and intertap interval (ITI) define the temporal relationship of a blink with respect to the reference tap, i.e., the tap preceding the blink. Note that the onset of the first pace within the resynchronization triad was synchronized with the actual tap (indicated by the curved arrow).

Fig. 2. Sample records of signals in Experiment 2 (strong tapping). The two upper panels show contact force signals of the right and left index fingers. The short vertical lines mark the onset (F_{on}), maximal value ($F_{\max}$), and offset (F_{off}) of force signals. The third and fourth panels depict corresponding finger position signals (PD_{on} - position down onset time, PU_{on} - position up onset time). The bottom panel depicts the vertical EOG signal indicating eye blinks (B_{on} - blink onset time, B_{off} - blink offset time). Note that the interblink interval (IBI) usually is around 3 s but for display purposes a special rare case with IBI = 1.1 s was selected for the graph.

Fig. 3. Examples of recorded contact force (first panel) and finger position signals (second panel) in the three experimental conditions of standard tapping (Experiment 1), strong tapping (Experiment 2), and impulse-like tapping (Experiment 3). Please note the different ordinate scaling. Abscissa scaling is 0.5 s.

Fig. 4. Phase resetting curve construction and basic interpretation. - *Construction*: (A) the three right panels schematically depict examples of blink occurrences elucidating the selection of the data points for the phase resetting curve. The blink event determines the corresponding *reference tap* (R) within the periodic tap series which, in turn, determines the *tap group* shown by the symbols in the shaded areas. (N.B., in Fig.4a, for visualization, different symbols (circles, stars, triangles) were used for the different tap groups, whereas in Figs.4B-D, the phase resetting curves, dots represent all tap groups.) The tap group consists of the two periodic taps preceding R and the three taps following R (the tap group represents a selection of periodic taps). Each tap group is then included in the phase resetting curve (left panel of Fig. 4) as six vertically aligned symbols (with the reference tap symbol aligned to time t = 0) at the abscissa value Φ which is determined by the interval t_b normalized to tapping period ISI (see Fig.1). Thus, all tap groups are plotted at their respective phases Φ for all eyeblinks, which by principle can occur at any phase Φ. The inclined dashed line above the abscissa indicates their locus of occurrence (from ($\Phi = 0, t = 0$) to (Φ = 1, t = ISI = 550 ms)). Note that $t = 0$ is defined by the reference tap R; negative time values denote taps preceding the reference tap whereas positive values denote taps following the reference tap. - *Basic interpretations of phase resetting curve*: (B) ideally, if tapping is not affected by the blinks and if blinks occur completely independent of the tapping process, the taps before and after the reference tap would form horizontal lines. (C) Any systematic deviation of the post-reference-taps (dot-lines above the abscissa) from the horizontal orientation indicates an influence of the blinks on the tapping rhythm. If the blink event fully resets the tapping oscillator, the next periodic tap would occur with a delay of one full ISI after the blink, thus these taps build the first inclined post-reference-tap dot-line (parallel to the inclined dashed line). (D) Any systematic deviation of a uniform (horizontal) distribution of the

dots over phase indicates the reverse effect of (C): the periodic tapping process controls the blink timing. Panel D shows an example where the blink onsets are synchronized with the undisturbed periodic tapping; therefore, dot locations are restricted to particular phases (here: $0 < \Phi < 0.2$).

Fig. 5. Phase resetting curve (A) and phase histogram (B) (frequency on ordinate is normalized to the total number of blinks) of the reference experiment of participant P1. The approximately uniform phase distribution (B) and the horizontal dot-lines in the curve (A) are consistent with the expected behaviour observed in independent processes.

Fig. 6. Phase resetting curves of all experimental data for the bimanual tapping. The row headers indicate the participants (P1-P7); the column numbers refer to Experiments 1, 2, and 3, respectively (see methods section for detailed description of the experiments.) The upper three dot-lines of all curves remain horizontal indicating that the tapping process is not significantly disturbed by the preceding spontaneous blinks. However, in most cases, the dot symbols are not uniformly distributed over phase, but show a higher density at small phase values. Presence of such preferred phases indicates that the onsets of the eyeblinks are entrained to some extent by the periodic taps.

Fig. 7. Phase histograms of eyeblinks in bimanual tapping. Ordinate scaling shows the frequency of occurrence in all panels. Data of the reference and (normal, strong, and impulse-like) tapping experiments are depicted for all participants (P1-P7). All histograms of tapping experiments show a clear shaping of the distributions compared to the approximate uniform distribution of

the corresponding reference experiment. Note that the scatter of the peaks of the phase histograms indicates individual internal delays.

Fig. 8. Phase histograms of eyeblinks during unimanual (A) and bimanual (B) tapping. Individual data of participant P1 are depicted; the column headers (normal, strong, and impulse-like) indicate Experiments 1, 2, and 3, respectively. Ordinate scaling shows the frequency of occurrence in all panels. All histograms show a clear shaping of the distributions, being more prominent in bimanual tapping.