



OPEN

SUBJECT AREAS:
PREMOTOR CORTEX
DECISIONReceived
20 February 2014Accepted
22 July 2014Published
13 August 2014Correspondence and
requests for materials
should be addressed to
X.L.F. (fuxl@psych.ac.
cn)

Voluntary Pressing and Releasing Actions Induce Different Senses of Time: Evidence from Event-Related Brain Responses

Ke Zhao^{1,2}, Ruolei Gu³, Liang Wang⁴, Ping Xiao⁵, Yu-Hsin Chen^{1,2}, Jing Liang^{1,2}, Li Hu⁵ & Xiaolan Fu¹

¹State Key Laboratory of Brain and Cognitive Science, Institute of Psychology, Chinese Academy of Sciences, Beijing, 100101, China, ²University of Chinese Academy of Sciences, Beijing, 100101, China, ³Key Laboratory of Behavior Science, Institute of Psychology, Chinese Academy of Sciences, Beijing, 100101, China, ⁴Key Laboratory of Mental Health, Institute of Psychology, Chinese Academy of Sciences, Beijing, 100101, China, ⁵Key Laboratory of Cognition and Personality of Ministry of Education, School of Psychology, Southwest University, Chongqing, 400715, China.

The timing intervals initiated by voluntary pressing actions are subjectively compressed compared with those initiated by voluntary releasing actions. Event-related potentials (ERPs) were employed in the present study to uncover the temporal mechanisms underlying this temporal illusion. The results revealed that the mean amplitude of the P1 component over the frontal-central recording sites, but not the P2 component, was larger in the voluntary pressing condition than in the voluntary releasing condition at the time perception stage. In the fronto-central region, increases in oscillatory activities of delta-theta frequency range (1-7 Hz) were found in the voluntary pressing condition, which corresponded with the emergence of the P1 peak. In addition, the P1 amplitude was negatively related to the corresponding reported time length at the single-trial level. These results are discussed in terms of the functional role of the response-locked P1 in the time perception stage.

Time interval estimation within a few hundred milliseconds is susceptible to different types of temporal illusions elicited by various factors (e.g., stimuli features, motion, and emotion)¹⁻⁵. One of these illusions is that the timing interval is experienced as shorter when it is induced by voluntary pressing compared with voluntary releasing actions⁶. In one of our previous studies, participants were asked to estimate the lengths of temporal intervals of which the start points were voluntary actions (pressing vs. releasing) and the endpoints were subsequent consequences. The reported intervals were shorter in the voluntary pressing condition than in both the voluntary releasing condition and the control condition when the timing intervals ranged from 250 to 1050 milliseconds⁶. This difference in the sense of time between two conditions is surprising and further investigation of this discrepancy may improve our understanding of subjective time perception and temporal judgments.

There has been ample evidence for the attentional allocation/distraction hypothesis, which states that attention plays a crucial role in the experience of temporal illusions⁷⁻¹¹. This hypothesis assumes that when fewer attentional resources are allocated to a time estimation task (e.g., when participants are distracted by an irrelevant task), fewer pulses are counted by the interoceptive “interval clock”, leading to an overall underestimation of time duration^{8,11-17}. In contrast, if participants are not distracted, more attentional capacity is available for temporal information processing, and the perceived time duration increases^{18,19}. This hypothesis is supported by previous studies using dual-task paradigms, in which one task is a time-relevant task (e.g., time estimation) and the other task is not (e.g., color judgment). The results indicated that subjective time was shorter when more attentional resources were allocated to the time-irrelevant task^{15,16}. This modulating effect on time perception could also be reflected in the voltage changes of ERPs components. For instance, two recent works revealed that when attention was distracted by a pitch discrimination task, underestimation of time was reflected in the behavioral results, and smaller contingent negative variation (CNV) amplitudes were found at fronto-central regions during the time perception stage^{20,21}.

As for the compressed interval related to the pressing condition compared to the releasing condition, the attentional allocation/distraction hypothesis might provide a reasonable explanation. To examine whether attention is distracted in the time perception stage, the ERPs were employed in the present study because their fine-grained temporal resolution enables the separation of neural signals in response to different events that occur very



close in time. However, unlike the stimulus-locked ERPs (including the CNV mentioned above), the stage of time perception for both voluntary pressing and releasing conditions is response-locked and ERP waveforms at this stage are unique. Among the major response-locked ERP components, the P1 and P2 most often appear in the interval between voluntary pressing action and subsequent outcome in response-locked ERP waveforms. In the experimental paradigms of motor movements, the P1 component ranged approximately 100 ms at the medial frontal cortex is correlated with corrected voluntary pressing action^{22–24}. This fronto-central distributed P1 might reflect an expectancy of a predicted action consequence. If there is a mismatch between the predicted action consequence and the sensory feedback, the P1 disappears. Instead, an erroneous response elicits an opposite polarity component with the same latency and scalp distribution, which is referred to as the error related negativity (ERN)^{25,26}. Similar to the P1 component, the P2 component might reflect the expectancy of a subsequent outcome at the same scalp distribution. This component is influenced by the contingency between a response and a subsequent consequence²⁷. Higher outcome probabilities result in larger amplitudes of P2^{28,29}.

According to the classic attention allocation/distraction hypothesis, the amount of attentional resources that are distracted from a time perception task might be reflected in the variation of fronto-central distribution of P1 and P2 components underlying the comparison of time perception stage between voluntary pressing and releasing conditions. To ensure the reliability of our results, we used two timing intervals between actions and delayed feedbacks (240–280 ms and 440–480 ms). To eliminate possible confounds (such as force intensity) between the two voluntary actions a voluntary pressing/releasing lever (VPRL for short, see Figure 1) was designed and applied. We hypothesized that the reported interval would be shorter in the voluntary pressing condition than in the voluntary releasing condition across the two timing intervals. In addition, the evoked amplitudes of P1 and P2 were expected to be different between the two experimental conditions. Meanwhile, as the information regarding oscillatory dynamics from the EEG signal is largely lost by the time-locked averaging of single trials in the traditional ERPs approach^{30,31}, this study also explored the dynamic oscillatory patterns in the EEG signal to uncover the differences between voluntary pressing and releasing conditions.

Results

Behavioral results. The main effect of “voluntary action” on reported time was significant, $F(1, 15) = 53.66$, $p < 0.001$, $\eta_p^2 = 0.78$. The perceived interval in the voluntary pressing condition ($M = 257.57$ ms, $SE = 12.11$ ms) was shorter than in the voluntary releasing condition ($M = 306.25$ ms, $SE = 11.92$ ms). The main effect of “timing interval” was also significant, $F(1, 15) = 16.91$, $p = 0.001$, $\eta_p^2 = 0.53$. The interaction between “voluntary action” and “timing interval” was not significant, $F(1, 15) < 0.001$, $p = 0.99$, $\eta_p^2 < 0.001$.

ERP Results. The P1 component. For the mean amplitude of P1, the main effect of “voluntary action” was significant, $F(1, 15) = 25.52$, $p < 0.001$, $\eta_p^2 = 0.63$. The P1 amplitude was significantly larger in the voluntary pressing condition ($M = 1.57$ μ V, $SE = 0.43$ μ V) than in the voluntary releasing condition ($M = -0.63$ μ V, $SE = 0.37$ μ V). Neither the main effect of “timing interval” ($F(1, 15) = 0.21$, $p = 0.66$, $\eta_p^2 = 0.01$) nor the interaction between two factors ($F(1, 15) = 0.11$, $p = 0.75$, $\eta_p^2 = 0.007$) was significant (see Figure 2).

The P2 component. For the mean amplitude of P2, there was no significant main effect of “voluntary action” ($F(1, 15) = 0.009$, $p = 0.93$, $\eta_p^2 = 0.001$) or “timing interval” ($F(1, 15) = 0.41$, $p = 0.53$, $\eta_p^2 = 0.03$), and their interaction was also not significant ($F(1, 15) = 0.12$, $p = 0.73$, $\eta_p^2 = 0.008$).

Time Frequency Results. For the baseline-corrected power at delta-theta frequencies (1–7 Hz) from 80 to 200 ms, the main effect of “voluntary action” was significant, $F(1, 15) = 8.81$, $p = 0.01$, $\eta_p^2 = 0.37$. Compared to the voluntary releasing condition ($M = 2.60$ μ V, $SE = 0.25$ μ V), a significant increase in delta-theta power was observed in the voluntary pressing condition ($M = 3.16$ μ V, $SE = 0.36$ μ V). Neither the main effect of “timing interval” ($F(1, 15) = 0.23$, $p = 0.64$, $\eta_p^2 = 0.02$) nor the interaction between the two factors ($F(1, 15) = 0.43$, $p = 0.52$, $\eta_p^2 = 0.03$) was significant (see Figure 3).

For the baseline-corrected phase-locking value (PLV) at delta-theta frequencies (1–7 Hz), the main effect of “region of interest” was significant, $F(1, 15) = 4.46$, $p = 0.05$, $\eta_p^2 = 0.23$. The interaction

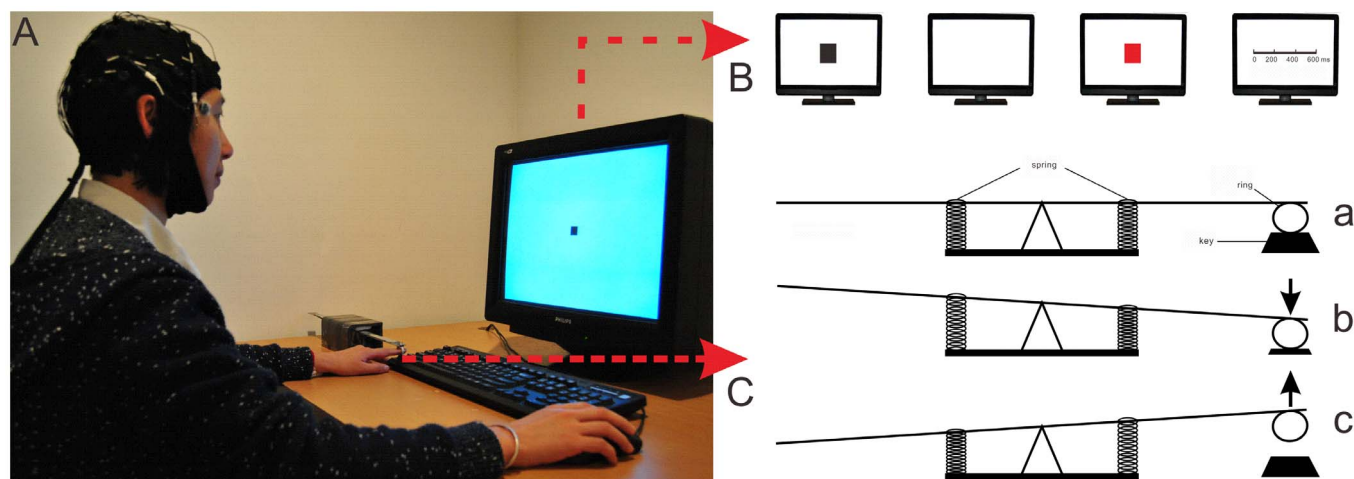


Figure 1 | Illustrations of the sequence of a single trial, experiment setup, and two conditions set in our experiment. (A) Illustration of the VPRL. Participants were asked to insert their left fore-finger into a metallic ring on the VPRL. **(B)** An illustration of a single trial; the S1 (black square), the timing interval followed by VPRL (red square), and the period in which participants were asked to make a judgment on the fourth screen. **(C).** A simplified illustration of the VPRL and demonstration for two conditions. **(a)** A simplified illustration of the VPRL, which composed of one lever, two springs, one metallic ring, and a bare frame; **(b)** An illustration of the voluntary pressing condition and an arrow representing the direction of force; **(c)** An illustration of the voluntary releasing condition and an arrow representing the direction of force.

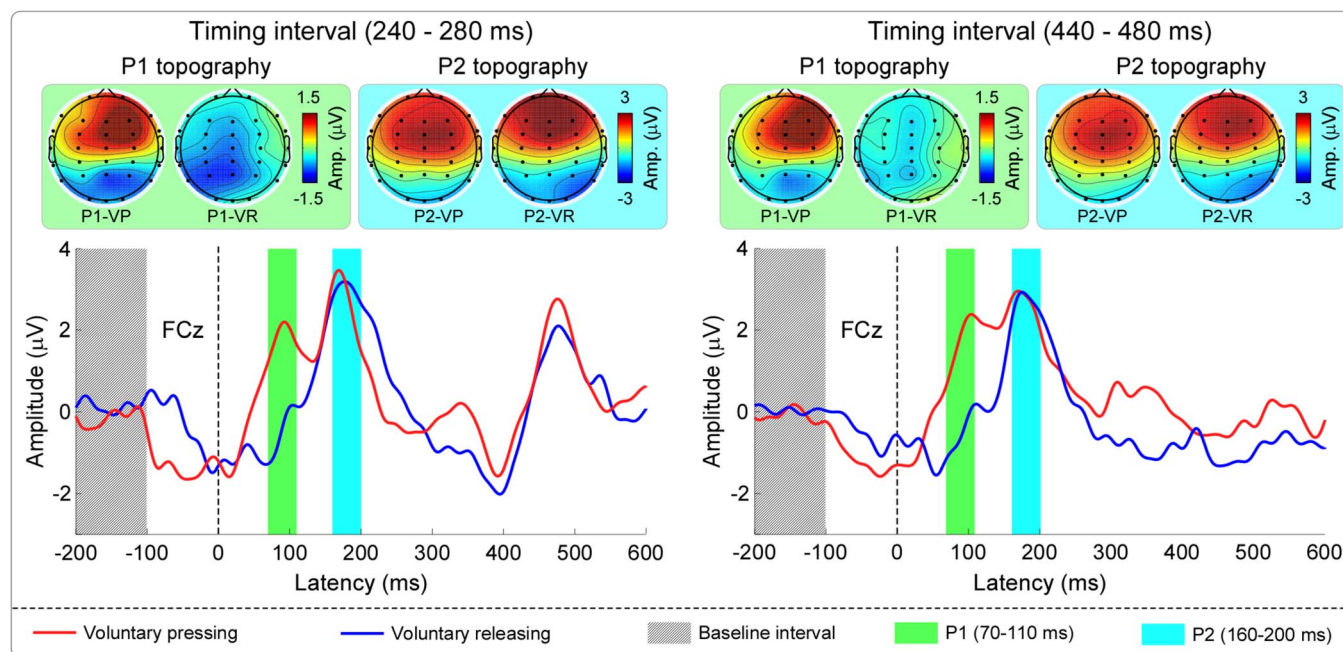


Figure 2 | The grand-average ERPs waveforms and scalp topographies in the voluntary pressing and releasing conditions at the FCz electrode. Top left: scalp topographies of P1 and P2 in the voluntary pressing condition and voluntary releasing condition when the timing interval is 240–280 ms. Top right: group average of ERPs in the voluntary pressing (VP) and voluntary releasing (VR) conditions is represented in red and blue waveforms, respectively. Top right and bottom right represents the scalp topographies and group average of ERPs in voluntary pressing and releasing conditions when the timing interval was 440–480 ms. The green and light-blue bars represent that the analyzed time window of P1 (70–110 ms) and P2 (160–200 ms), respectively. The baseline is marked in gray.

between the “region of interest” and “voluntary action” was also significant, $F(1, 15) = 28.82, p < 0.001, \eta_p^2 = 0.66$. Post hoc pairwise comparisons indicated that the PLV was smaller in the voluntary pressing condition than in the voluntary releasing condition at the Fz electrode, $t(15) = -2.17, p = 0.04$. However, the PLV was marginally larger in the voluntary pressing condition than in the voluntary releasing condition at the C4 electrode, $t(15) = 1.94, p = 0.07$. There was no significant main effect of “voluntary action” ($F(1, 15) = 0.002, p = 0.97, \eta_p^2 < 0.001$) or “timing interval” ($F(1, 15) = 0.18, p = 0.68, \eta_p^2 = 0.01$), and their interaction was also not significant ($F(1, 15) = 0.18, p = 0.67, \eta_p^2 = 0.01$). The interaction between “timing interval” and “region of interest” was also not significant ($F(1, 15) = 0.90, p = 0.36, \eta_p^2 = 0.06$; see Figure 4).

Single-trial analysis of the relationship between P1 amplitude and reported interval. We adopted linear mixed models (LMM) to further explore the relationship between the behavioral variables of estimation of time interval and P1 amplitude at the single-trial level (Figure 5). The P1 amplitude was negatively related to the reported interval (such effect was maximal at FCz, from 45 to 103 milliseconds; t -value = $-3.24, p = 0.005$). This observation indicated that, at a within-individual level, trials with a larger P1 amplitude normally had a shorter reported time interval.

Discussion

In the present study, the ERP measurements, including the P1 and P2 components, were employed to compare different temporal courses between voluntary pressing and releasing conditions in the stages of time perception. Participants were asked to directly estimate the same timing intervals under two conditions (voluntary pressing vs. voluntary releasing) when the timing interval was set to 240–280 ms or 440–480 ms. The reported time was consistently compressed in the voluntary pressing condition compared to the voluntary releasing condition.

Regarding the ERP results for the time perception stage, a larger P1 was found in the voluntary pressing condition than in the voluntary releasing condition regardless of the length of the timing interval. These differences were maximal at the fronto-central region. In addition, the subjective time and P1 amplitude were significantly related at the single-trial level, i.e., the higher the amplitude of P1 the shorter the estimated interval. According to attentional allocation/distraction hypothesis, this P1 component, which captured a fronto-central distribution similar to the CNV in stimulus-locked ERP studies, might be an index of attentional allocation in the time perception stage. In previous studies, the P1 was observed following corrected pressing actions^{22–24}. However, to our knowledge, no study has ever used the releasing action to investigate P1 amplitudes. The enhancement of P1 in the voluntary pressing condition might reflect that the attention to time events was diverted, thus resulting in underestimation of the timing interval. One might argue that this P1 component represents motor activity per se, such that the P1 finding in this study merely reflects different forms of motor activity in two conditions. We disagree with this viewpoint for the following reasons. First, during the experiment, participants were instructed to press or release the left CTRL key with their left fore-fingers. Presumably, the motor activity generated by the movement of this finger should be asymmetrically distributed, i.e., showing a brain response maximally distributed at the hemisphere contralateral to the moved hand/finger (e.g., primary motor cortex, around C4 electrode in the present study). In contrast, the detected P1 wave, as well as the difference of P1 between two conditions (pressing vs. releasing), was maximally distributed at the fronto-central region, which deviated from the motor-related brain regions.

Second, as revealed by the PLV results, the difference in PLV between the voluntary left pressing condition and the voluntary left releasing condition at the delta-theta band (1–7 Hz) was maximal at the contralateral-central region (i.e., maximal around C4 electrode). The scalp distribution of the PLV difference matched well with the configuration of the motor activity, indicating that the movement of

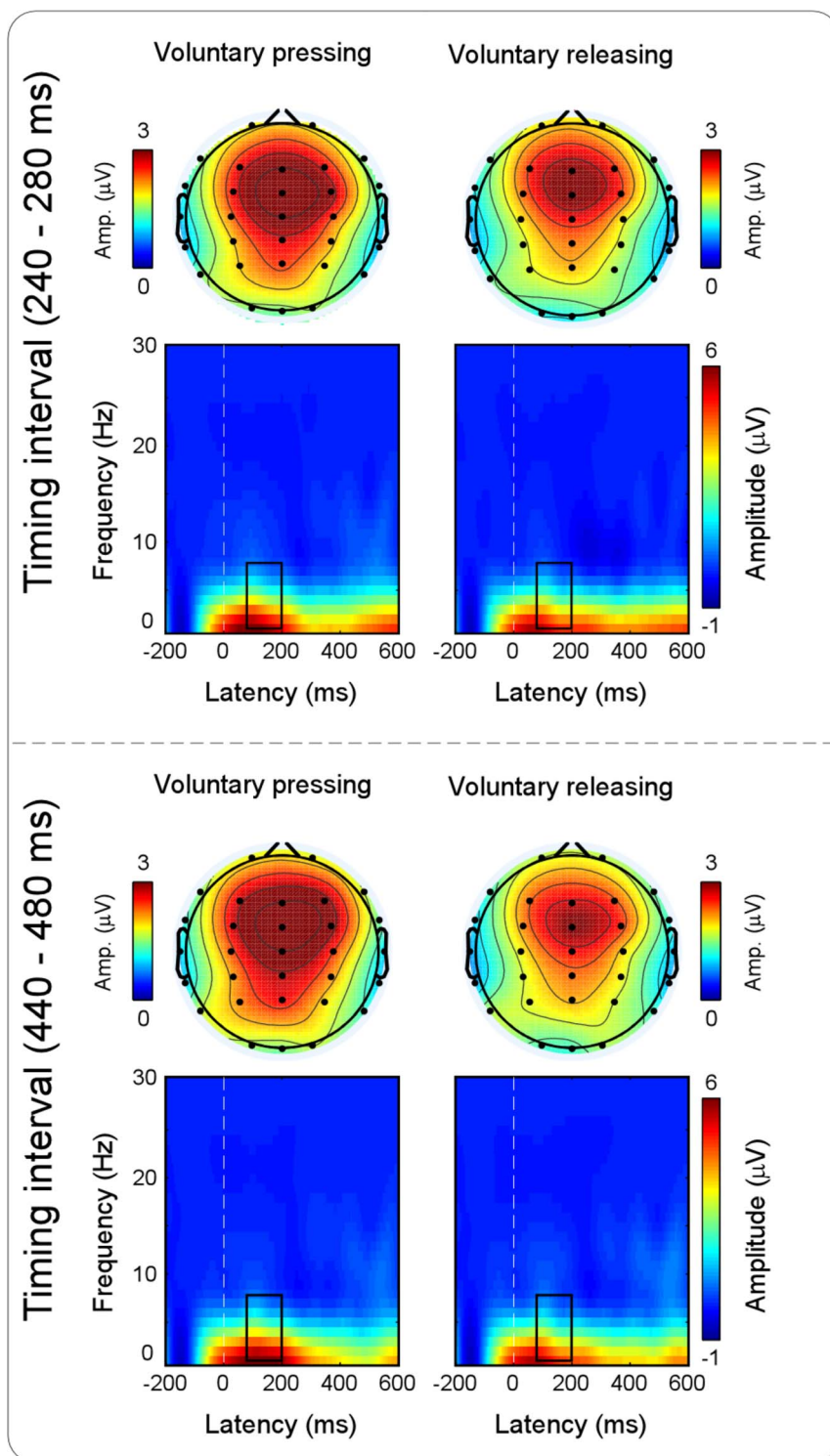


Figure 3 | Time-frequency representations of oscillatory power in voluntary pressing and releasing conditions at the FCz electrode. Top panel is a description when the timing interval is 240–280 ms, whereas the bottom panel is for 440–480 ms. Top row of top panel: topographies of the delta-theta band (1–7 Hz) at the 80–200 ms for two conditions (voluntary pressing and releasing condition) and difference between two conditions. The bottom row of the top panel represents the oscillatory power for both voluntary pressing and releasing condition. Time-frequency plots separately for voluntary pressing and releasing conditions.

the participants' left fore-fingers elicited changes in brain responses. These changes were captured in the phase space (indexed by delta-theta PLV) rather than in the power space (indexed by P1 amplitude and delta-theta power). The mismatch between the scalp distribution of P1 (and delta-theta power; maximal at fronto-central region) and delta-theta PLV (maximal at contralateral-central region) indicated

that P1 and delta-theta power were minimally involved in the motor processing.

Finally, the appearance of the P1 corresponded with increased delta-theta power, which contrasts with previous findings that motor activity is associated with beta band rhythm^{32–35}. Furthermore, the focal spatial and spectral distribution of the delta-theta responses

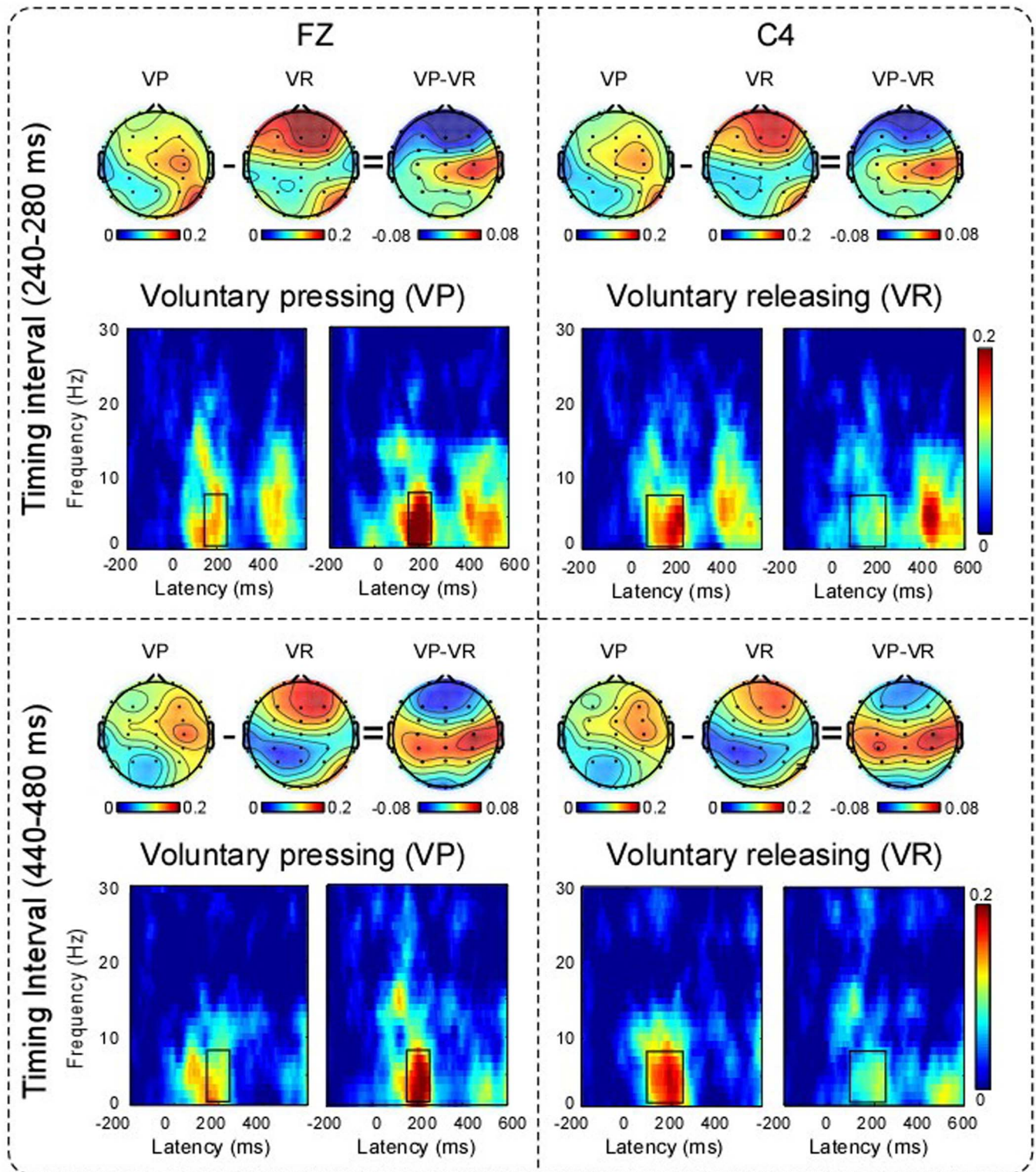


Figure 4 | Time-frequency representations of phase-locking value in voluntary pressing (VP) and releasing (VR) conditions at the Fz and C4 electrodes. Top panel is a description when the timing interval is 240–280 ms, whilst the bottom panel is for 440–480 ms. Top left: PLV of the delta-theta band (1–7 Hz) at the 170–220 ms for two conditions (voluntary pressing and releasing condition) and difference (VP-VR) between two conditions when the timing interval is 240–280 ms. Bottom left: PLV of the delta-theta band (1–7 Hz) at the 170–220 ms for two conditions (voluntary pressing and releasing condition) and difference between two conditions when the timing interval is 440–480 ms. Top right: PLV of the delta-theta band (1–7 Hz) at the 80–200 ms for two conditions (voluntary pressing and releasing condition) and difference between two conditions when the timing interval is 240–280 ms. Bottom right: PLV of the delta-theta band (1–7 Hz) at the 80–200 ms for two conditions (voluntary pressing and releasing condition) and difference between two conditions when the timing interval is 440–480 ms.

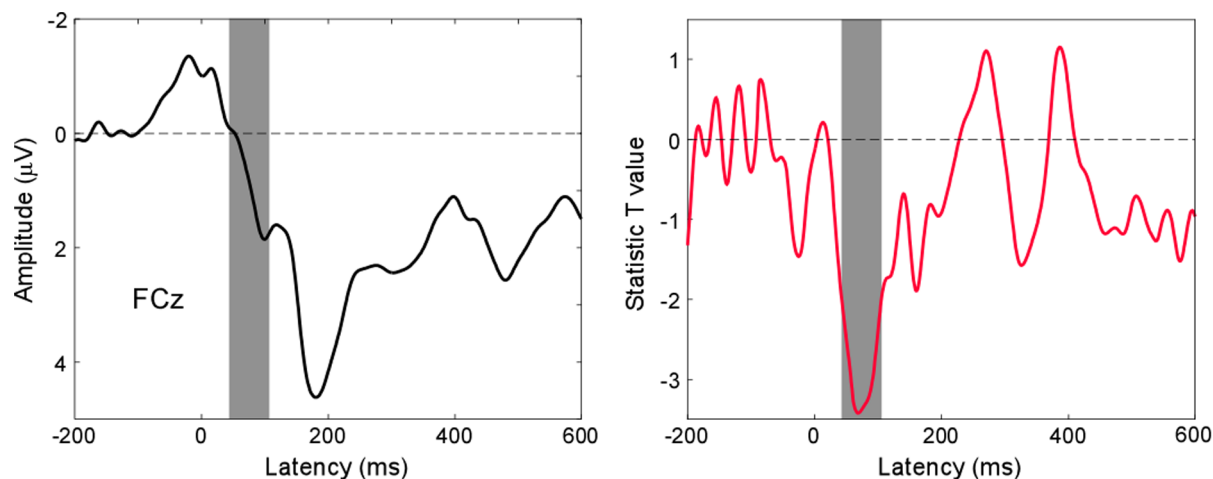


Figure 5 | Group-level average of waveform at FCz of all participants (left panel). Right panel shows the statistic t-value, revealed by the linear mixed model, showing a negative and significant relationship between P1 amplitude and reported interval, with the maximum from 45 to 103 ms (gray area in both panels).

with a maximum at fronto-central electrodes argues against the possibility that the responses were due to muscle activity.

What is the reason for the difference in attentional allocations between voluntary pressing and voluntary releasing conditions? One possible explanation involves differences between the after-action effects of the two actions. According to the internal models of motor control^{36–38}, an efferent copy of a motor command enables the neural system to generate the expectancy of the predicted consequences of one's action before the actual feedback (see Figure 6). In our paradigm, the sensory feedback of the current action is delayed (see the Methods section) while the expectancy of predicted consequences from the efferent copy remains. Most importantly, the degree of expectancy between voluntary pressing and releasing is different. In daily life, the action of pressing is practiced more frequently and is often associated with timely feedback⁶. Thus, the prediction of feedback and the actual sensory feedback are frequently compared to optimize future predictions. In contrast, the action of releasing is seldom practiced and is not always accompanied by immediate consequences, as is the action of pressing. That is to say, the prediction is less optimized through this comparison. Hence, the expectancy of predicted consequences for the voluntary pressing action is influenced more strongly by previous experiences^{39,40} than is the voluntary releasing action. This enhanced expectancy may distract attention away from the temporal events in the stage of time perception, which leads to an underestimation of temporal intervals^{4,15}. In short, a higher degree of expectancy is

diverted to a break in the voluntary pressing condition, resulting in less attentional resources being allocated to time estimation and the perception of a shorter interval.

This speculation was also supported by spectral results, as the delta-theta power in the pressing cognition was enhanced compared to the releasing condition across the two timing intervals. These results seem to be responsible for the differences in amplitude in medial frontal region activities between voluntary pressing and releasing conditions. Specifically, the delta-theta frequency band has been found to be correlated with somatosensory expectations⁴¹. Meanwhile, theta and delta power enhancements have been associated with anticipation of upcoming events^{42,43}. Thus the oscillation data support the viewpoint that increasing the expectancy of the predicted action consequence distracts more attention and results in shorter estimation of the time interval.

In addition, a P2 with fronto-central distribution was elicited for both conditions in the time perception stage. The amplitude showed no difference between voluntary pressing and releasing conditions regardless of the length of the time interval, which ranged from 240 to 280 ms or from 440 to 480 ms. Given that the contingency between the action and subsequent consequence was similar for the two conditions in this study, it is not surprising that no difference was found in this component. This result echoed a recent study in which tones coinciding with pressing or releasing actions elicited similar patterns of EEG waveforms⁴⁴. Thus, we suggest that the different senses of time between voluntary pressing and releasing were not induced by the contingency between action and delayed outcome.

In summary, the behavioral results replicated findings suggesting that voluntary pressing and voluntary releasing actions correspond to different senses of elapsed time⁶, which is echoed by the compression effect associated with voluntary pressing actions^{5,45–53}. Through the ERP technique, we found a difference in P1 between voluntary pressing and voluntary releasing conditions in the time perception stage. In addition, delta-theta band activity was consistently enhanced in the pressing condition across the two time intervals. These results suggested that the larger P1 with fronto-central distribution in the pressing condition might reflect that more attention was distracted from time perception, which resulted in shorter perceived interval between the pressing action and its following consequence.

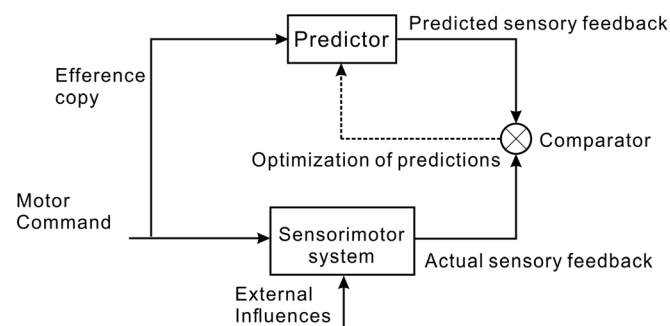


Figure 6 | A model determined the sensory consequences of an action³⁶. An internal clock makes predictions of the sensory feedback based on the motor command. These predictions are then compared with the actual sensory feedback to optimize predictors of future experience.

Methods

Ethics Statement. The experiment was conducted in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Institute of Psychology,



Chinese Academy of Sciences. All participants gave written informed consent prior to the experiment and were paid for their participation.

Participants. Sixteen right-handed, healthy volunteers (6 females; mean age: 22.69 ± 2.02 years) participated in the experiment. All had normal or corrected-to-normal vision and had not previously participated in any experiment related to time estimation.

Experimental tasks and procedure. A 17-inch cathode-ray tube (CRT) monitor running at a refresh rate of 85 Hz with a resolution of 1024 × 768 pixels as well as the software package E-prime 2.0 (Psychology Software Tools, Inc.), were used for stimuli presentation and behavioral data collection in our experiment. All participants were seated in a sound attenuated room, approximately 70 cm from the presentation screen. The experiment consisted of two conditions, voluntary pressing and voluntary releasing (see Figure 1).

Voluntary Pressing Condition. Upon presentation of a black square (stimulus 1, “S1” for short; size: 1 cm × 1 cm) at the center of the screen, participants were asked to relax and insert their left fore-finger into a metallic ring on the VPRL (see Figure 1). Participants were asked to press the left CTRL key whenever they intended to make a response. To prevent unconscious or accidental pressing and possible mistakes, we set an initial period of 500 ms during which pressing of the left CTRL key would incur a warning that asked participants to restart the current trial. When the left CTRL key was pressed after the warning period, the black square would disappear simultaneously with the response, followed by a blank screen that lasted for a random interval (240–280 ms or 440–480 ms). Thereafter, a red square (stimulus 2, “S2”; size: 1 cm × 1 cm) appeared at the center of the screen for 500 ms. Participants were then asked to estimate the interval between the time points at which the black square disappeared and the red square appeared by using the mouse to click on a continuous time scale (ranging from 0 to 600 ms with 5 markers each represented 100 ms divisions). Participants were asked to click anywhere on the scale to give a precise answer. The time scale remained visible until the response was made. Afterwards, an inter-trial interval that ranged randomly from 1800 ms to 2400 ms was presented (Figure 1B).

Voluntary Releasing Condition. Participants were asked to relax and insert their left fore-finger into a metallic loop on the VPRL. A blank screen was presented indefinitely until the participants pressed and held down the left CTRL key which elicited the presentation of S1 (size: 1 cm × 1 cm) at the center of the screen. Participants were asked to release the left CTRL key whenever they intended to make a response. Once the left CTRL key was voluntarily lifting the finger or wrist after at least 500 ms was released (similar to that of the pressing condition), the black square disappeared immediately. The rest of the procedure was similar to that of the voluntary pressing condition after the blank screen was presented.

In this study, the combination of two types of timing intervals (240–280 ms, 440–480 ms) and 2 two types of voluntary actions (voluntary pressing, voluntary releasing) resulted in four individual blocks in total. Each block consisted of 50 trials (200 trials in total). The sequence of the four blocks was counterbalanced across the participants.

Prior to the formal experiment, participants were given time to become familiar with the VPRL and experiment procedure. They were required to watch 12 examples of different timing intervals ranging from 100 to 600 ms to practice estimating time intervals. Participants who reported being unfamiliar with different types of time intervals were instructed to repeat this practice. Participants practiced four trials of each condition to familiarize themselves with the apparatus, procedure, and tasks. In the formal task, we calculated ERPs aligned with the disappearance of the S1 (the black square) to test the temporal course of different conditions.

As for the behavioral results, the reported time was compared using a two-way repeated-measures analysis of variance (ANOVA), with “voluntary action” (two levels: pressing vs. releasing) and “timing interval” (two levels: 240–280 ms vs. 440–480 ms) as within-subject factors. All statistical analysis was performed using SPSS (17.0; SPSS, Inc., Chicago, IL).

EEG recordings and data analysis. EEG data were acquired using a 32-channel NuAmps Quickcap, 40-channel NuAmps DC amplifier, and Scan 4.5 Acquisition Software (Compumedics Neuroscan, Inc.). EEG data were collected from 32 scalp electrodes (Fp1, Fp2, F7, F8, F3, F4, FT7, FT8, T3, T4, FC3, FC4, C3, C4, CP3, CP4, TP7, TP8, T5, T6, P3, P4, O1, O2, Fz, FCz, Cz, CPz, Pz, Oz, A1, A2) according to the international 10–20 system. The sampling rate was 1000 Hz. Horizontal electrooculograms (HEOGs) were recorded from electrodes placed at the outer canthi of both eyes. Vertical electrooculograms (VEOGs) were recorded from electrodes placed above and below the left eye. All EEG data that were right mastoid referenced on-line were re-referenced off-line to the averaged mastoid reference by subtracting one half of the activity recorded at the right mastoid from each sample of the data of each channel.

During the off-line analysis, ocular artifacts were removed using independent component analysis (ICA) decomposition implemented in the EEGLAB toolbox⁵⁴, an open source toolbox running in the MATLAB environment. Continuous EEG data were band-pass filtered between 1 and 30 Hz. EEG epochs were extracted using a window of 800 ms (200 ms before the disappearance of S1 and 600 ms after the disappearance of S1) and baseline was corrected using the pre-stimulus interval (–200 to –100 ms).

Because both P1 and P2 were observed to be maximal at medial frontal cortex, their amplitudes were obtained by calculating the mean amplitudes within their respective time intervals (P1: 70–110 ms; P2: 160–200 ms) at the FCz electrode. The amplitudes of P1 and P2 were compared using a two-way repeated-measures analysis of variance (ANOVA) with “voluntary action” (two levels: pressing vs. releasing) and “timing interval” (two levels: 240–280 ms vs. 440–480 ms) as factors.

Time-frequency distributions (TFDs: both power and phase-locking value (PLV)) of the EEG time course were obtained using a windowed Fourier transform (WFT) with a fixed 250 ms Hanning window⁵⁵. These parameters allow achieving a good tradeoff between time resolution and frequency resolution within the explored range of frequencies⁵⁶. TFDs were then baseline-corrected (reference interval: –200 to –100 ms) at each explored frequency using subtraction approach⁵⁷, which has been verified as an unbiased baseline correction strategy^{55,57}. For each subject and each experimental condition, we extracted the baseline-corrected power at delta-theta frequencies (1–7 Hz) from 80 to 200 ms. Similar with ERPs, the obtained powers were compared using a two-way repeated-measures ANOVA, with “voluntary action” (two levels: pressing vs. releasing) and “timing interval” (two levels: 240–280 ms vs. 440–480 ms) as factors.

As for the PLV (phase-locking value), we conducted a three-way repeated-measures ANOVA, with “voluntary action” (two levels: pressing vs. releasing), “region of interest” (two electrodes: Fz vs C4) and “timing interval” (two levels: 240–280 ms vs. 440–480 ms) as factors. We extracted the baseline-corrected PLV at delta-theta frequencies (1–7 Hz) for Fz (170–220 ms) and C4 (80–200 ms), respectively. When an interaction was significant, post hoc pairwise comparisons was performed.

For each electrode and each time bin of the P1 waveform, the relationship between P1 amplitude and reported interval was assessed using linear mixed models. This procedure yielded time-courses of T-value, representing the strength of the relationship between P1 signal amplitude and reported intervals. To address the problem of multiple comparisons, the significance level (P-value) was corrected using a false discovery rate procedure^{58,59}.

- Eagleman, D. M. Human time perception and its illusions. *Curr. Opin. Neurobiol.* **18**, 131–136 (2008).
- Fraisse, P. Perception and estimation of time. *Annu. Rev. Psychol.* **35**, 1–37 (1984).
- Droit-Volet, S. & Meck, W. H. How emotions colour our perception of time. *Trends Cogn. Sci.* **11**, 504–513 (2007).
- Ross, J., Morrone, M. C., Goldberg, M. E. & Burr, D. C. Changes in visual perception at the time of saccades. *Trends Neurosci.* **24**, 113–121 (2001).
- Haggard, P., Clark, S. & Kalogeras, J. Voluntary action and conscious awareness. *Nat. Neurosci.* **5**, 382–385 (2002).
- Zhao, K., Chen, Y.-H., Yan, W.-J. & Fu, X. To Bind or Not to Bind? Different Temporal Binding Effects from Voluntary Pressing and Releasing Actions. *PLoS One* **8**, e64819 (2013).
- Treisman, M. Temporal discrimination and the indifference interval: Implications for a model of the “internal clock”. *Psychol. Monogr.* **77**, 1–31 (1963).
- Buhusi, C. V. & Meck, W. H. Relative time sharing: new findings and an extension of the resource allocation model of temporal processing. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **364**, 1875–1885 (2009).
- Renoult, L., Roux, S. & Riehle, A. Time is a rubberband: neuronal activity in monkey motor cortex in relation to time estimation. *Eur. J. Neurosci.* **23**, 3098–3108 (2006).
- Mattes, S. & Ulrich, R. Directed attention prolongs the perceived duration of a brief stimulus. *Percept. Psychophys.* **60**, 1305–1317 (1998).
- Tse, P. U., Intriligator, J., Rivest, J. & Cavanagh, P. Attention and the subjective expansion of time. *Percept. Psychophys.* **66**, 1171–1189 (2004).
- Brown, S. W. Time perception and attention: The effects of prospective versus retrospective paradigms and task demands on perceived duration. *Percept. Psychophys.* **38**, 115–124 (1985).
- Coull, J. T., Vidal, F., Nazarian, B. & Macar, F. Functional anatomy of the attentional modulation of time estimation. *Science* **303**, 1506–1508 (2004).
- Fortin, C., Bédard, M.-C. & Champagne, J. Timing during interruptions in timing. *J. Exp. Psychol. Hum. Percept. Perform.* **31**, 276–288 (2005).
- Fortin, C. et al. Expectancy in humans in multisecond peak-interval timing with gaps. *Atte. Perce. Psycho.* **71**, 789–802 (2009).
- Macar, F., Grondin, S. & Casini, L. Controlled attention sharing influences time estimation. *Mem. Cognit.* **22**, 673–686 (1994).
- Zakay, D. & Block, R. A. The role of attention in time estimation processes. *Adv. In Psychology* **115**, 143–164 (1996).
- Thomas, E. A. & Weaver, W. B. Cognitive processing and time perception. *Percept. Psychophys.* **17**, 363–367 (1975).
- Hicks, R. E., Miller, G. W., Gaes, G. & Bierman, K. Concurrent processing demands and the experience of time-in-passing. *Am. J. Psychol.* **431**–446 (1977).
- Chen, Y. et al. Attentional Modulation of Time Perception: An ERP Study (in Chinese). *Acta. Psychologica. Sinica.* **39**, 1002–1011 (2007).
- Liu, Y. et al. The attention modulation on timing: an event-related potential study. *PLoS One* **8**, e66190 (2013).
- de Bruijn, E. R., Miedl, S. F. & Bekkering, H. How a co-actor’s task affects monitoring of own errors: evidence from a social event-related potential study. *Exp. Brain Res.* **211**, 397–404 (2011).
- Gehring, W. J., Goss, B., Coles, M. G., Meyer, D. E. & Donchin, E. A neural system for error detection and compensation. *Psychol. Sci.* **4**, 385–390 (1993).



24. Torpey, D. C., Hajcak, G., Kim, J., Kujawa, A. & Klein, D. N. Electro cortical and behavioral measures of response monitoring in young children during a Go/No-Go task. *Dev. Psychobiol.* **54**, 139–150 (2012).
25. Falkenstein, M., Hoormann, J., Christ, S. & Hohnsbein, J. ERP components on reaction errors and their functional significance: a tutorial. *Biol. Psychol.* **51**, 87–107 (2000).
26. Falkenstein, M., Hohnsbein, J., Hoormann, J. & Blanke, L. Effects of errors in choice reaction tasks on the ERP under focused and divided attention. *Psychophysiological brain research* **1**, 192–195 (1990).
27. Nikolaev, A. R., Ziesler, M., Dimova, K. & van Leeuwen, C. Anticipated action consequences as a nexus between action and perception: evidence from event-related potentials. *Biol. Psychol.* **78**, 53–65 (2008).
28. Eppinger, B., Kray, J., Mock, B. & Mecklinger, A. Better or worse than expected? Aging, learning, and the ERN. *Neuropsychologia* **46**, 521–539 (2008).
29. n  nuez Castellar, E., K  hn, S., Fias, W. & Notebaert, W. Outcome expectancy and not accuracy determines posterror slowing: ERP support. *Cogn. Affect Behav. Neurosci.* **10**, 270–278 (2010).
30. Makeig, S. *et al.* Electroencephalographic brain dynamics following manually responded visual targets. *PLoS Biol.* **2**, e176 (2004).
31. Pfurtscheller, G. & Aranibar, A. Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalogr. Clin. Neurophysiol.* **42**, 817–826 (1977).
32. Pfurtscheller, G. Central beta rhythm during sensorimotor activities in man. *Electroencephalogr. Clin. Neurophysiol.* **51**, 253–264 (1981).
33. McFarland, D. J., Miner, L. A., Vaughan, T. M. & Wolpaw, J. R. Mu and beta rhythm topographies during motor imagery and actual movements. *Brain Topogr.* **12**, 177–186 (2000).
34. Pfurtscheller, G., Stancaek Jr, A. & Neuper, C. Post-movement beta synchronization. A correlate of an idling motor area? *Electroencephalogr. Clin. Neurophysiol.* **98**, 281–293 (1996).
35. Ohara, S. *et al.* Movement-related change of electrocorticographic activity in human supplementary motor area proper. *Brain* **123**, 1203–1215 (2000).
36. Blakemore, S.-J., Wolpert, D. & Frith, C. Why can't you tickle yourself? *Neuroreport* **11**, 11–16 (2000).
37. Miall, R. & Wolpert, D. M. Forward models for physiological motor control. *Neural Networks* **9**, 1265–1279 (1996).
38. Wolpert, D. M. & Flanagan, J. R. Motor prediction. *Curr. Biol.* **11**, 729–732 (2001).
39. Ebert, J. P. & Wegner, D. M. Time warp: Authorship shapes the perceived timing of actions and events. *Conscious. Cogn.* **19**, 481–489 (2010).
40. Witney, A. G., Vetter, P. & Wolpert, D. M. The influence of previous experience on predictive motor control. *Neuroreport* **12**, 649–653 (2001).
41. Babiloni, C. *et al.* Anticipation of somatosensory and motor events increases centro-parietal functional coupling: an EEG coherence study. *Clin. Neurophysiol.* **117**, 1000–1008 (2006).
42. Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I. & Schroeder, C. E. Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* **320**, 110–113 (2008).
43. van Wingerden, M., Vinck, M., Lankelma, J. & Pennartz, C. M. Theta-band phase locking of orbitofrontal neurons during reward expectancy. *J. Neurosci.* **30**, 7078–7087 (2010).
44. Horv  th, J. Action-sound coincidence-related attenuation of auditory ERPs is not modulated by affordance compatibility. *Biol. Psychol.* **93**, 81–87 (2013).
45. Aarts, H. & van den Bos, K. On the foundations of beliefs in free will intentional binding and unconscious priming in self-agency. *Psychol. Sci.* **22**, 532–537 (2011).
46. Buehner, M. J. & Humphreys, G. R. Causal binding of actions to their effects. *Psychol. Sci.* **20**, 1221–1228 (2009).
47. Cravo, A. M., Claessens, P. M. & Baldo, M. V. Voluntary action and causality in temporal binding. *Exp. Brain Res.* **199**, 95–99 (2009).
48. Engbert, K. & Wohlschl  ger, A. Intentions and expectations in temporal binding. *Conscious. Cogn.* **16**, 255–264 (2007).
49. Engbert, K., Wohlschl  ger, A. & Haggard, P. Who is causing what? The sense of agency is relational and efferent-triggered. *Cognition* **107**, 693–704 (2008).
50. Humphreys, G. R. & Buehner, M. J. Magnitude estimation reveals temporal binding at super-second intervals. *J. Exp. Psychol. Hum. Percept. Perform.* **35**, 1542–1549 (2009).
51. Moore, J. & Haggard, P. Awareness of action: Inference and prediction. *Conscious. Cogn.* **17**, 136–144 (2008).
52. Moore, J. W., Wegner, D. M. & Haggard, P. Modulating the sense of agency with external cues. *Conscious. Cogn.* **18**, 1056–1064 (2009).
53. Walsh, E. & Haggard, P. Action, prediction, and temporal awareness. *Acta Psychol (Amst)*. **142**, 220–229 (2013).
54. Delorme, A. & Makeig, S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Meth.* **134**, 9–21 (2004).
55. Hu, L., Xiao, P., Zhang, Z., Mouraux, A. & Iannetti, G. Single-trial time-frequency analysis of electrocortical signals: Baseline correction and beyond. *NeuroImage* **84**, 876–887 (2014).
56. Zhang, Y. D., Amin, M. G. & Himed, B. Joint DOD/DOA estimation in MIMO radar exploiting time-frequency signal representations. *Eurasip. J. Adv. Sig. Pr.* **2012**, 1–10 (2012).
57. Hu, L., Peng, W., Valentini, E., Zhang, Z. & Hu, Y. Functional features of nociceptive-induced suppression of alpha band electroencephalographic oscillations. *J. Pain* **14**, 89–99 (2013).
58. Genovese, C. R., Lazar, N. A. & Nichols, T. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage* **15**, 870–878 (2002).
59. Caty, G., Hu, L., Legrain, V., Plaghki, L. & Mouraux, A. Psychophysical and electrophysiological evidence for nociceptive dysfunction in complex regional pain syndrome. *Pain* **154**, 2521–2528 (2013).

Acknowledgments

This work was supported in part by grants from 973 Program (2011CB302201) and the National Natural Science Foundation of China (61075042). The authors sincerely thank Dr. Wen-jing Yan's help in the early stages of preparing the manuscript.

Author contributions

K.Z. and X.L.F. had the idea and design the experiments; K.Z. and Y.C. prepared the experimental setup; K.Z., J.L. and Y.C. collected the data; K.Z., J.L., L.H. and P.X. analyzed all the data; K.Z., X.L.F., L.H., R.L.G., L.W. and J.L. wrote the paper.

Additional information

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Zhao, K. *et al.* Voluntary Pressing and Releasing Actions Induce Different Senses of Time: Evidence from Event-Related Brain Responses. *Sci. Rep.* **4**, 6047; DOI:10.1038/srep06047 (2014).



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder in order to reproduce the material. To view a copy of this license, visit <http://creativecommons.org/licenses/by-nc-sa/4.0/>