Journal Club

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Beta Rebound in Visuomotor Adaptation: Still the Status Quo?

Liyu Cao[1] and Yi-Ming Hu[2,3]

[1]School of Psychology, University of Glasgow, Glasgow G12 8QB, United Kingdom, [2]Research Institute of Information Technology, Tsinghua University, Beijing 100084, Peoples' Republic of China, and [3]Max Planck Institute for Gravitational Physics (Albert Einstein Institute), D-30167 Hannover, Germany

Review of Tan et al.

Oscillatory activity is a prominent feature of electromagnetic signals measured from the brain. Among others, beta oscillations (13–30 Hz) have been extensively investigated in the context of movements. Upon completion of a movement (e.g., a finger extension), an increase of beta power relative to baseline is consistently observed (Pfurtscheller et al., 1996). This is often referred to as post-movement beta synchronization/rebound, or simply beta rebound. A sensorimotor origin of beta rebound has been confirmed in human neuroimaging studies (Jurkiewicz et al., 2006; Parkes et al., 2006). The functional role of beta rebound is still under debate, but it has been hypothesized to have a role in actively keeping the status quo of the motor system (Pogosyan et al., 2009; Engel and Fries, 2010) or in assisting sensory processing (Cassim et al., 2001; Reyns et al., 2008). In a recent study, Tan et al. (2016) showed a close relationship between the amplitude of beta rebound and participants' confidence in predicting the position of a joystick controlled cursor on the screen. Specifically, higher beta rebound was associated with a higher confidence level.

Received March 27, 2016; revised May 13, 2016; accepted May 14, 2016.

We thank Joachim Gross for helpful comments on an earlier draft of the paper.

The authors declare no competing financial interests.

Correspondence should be addressed to Liyu Cao, School of Psychology, University of Glasgow, Glasgow, G12 8QB, UK. E-mail: liyuc@psy.gla.ac.uk.

DOI:10.1523/JNEUROSCI.1007-16.2016

 0270-6474/16/366365-03$15.00/0

In the study, participants used a finger-joystick to move a cursor from the center of the screen to the position of a target dot (Tan et al., 2016, their Fig. 1*A*). In each trial, the target dot randomly appeared at one of eight positions equally dispersed around the periphery of the screen. By systematically manipulating the correspondence between the angular displacement of the joystick and the direction of cursor movement, the authors induced different magnitudes of performance errors (i.e., the angle between the line connecting cursor starting position and cursor final position and the line connecting cursor starting position and target position) throughout the testing session. Then the authors performed a Bayesian learning modeling analysis of performance errors to assess participants' uncertainties in predicting the cursor movement. For each trial, this analysis generates a probability distribution, of which each point represents the probability of a pair of mean and variance of performance errors. The area covering 80% of total probability represents estimation uncertainty, which is related to participants' confidence of predicting the final position of the cursor from joystick movement (i.e., to what extent participants know the relationship between the cursor position and joystick movement). The variance in the maximal probability point represents expected uncertainty and it reflects possible perturbations in the external environment (i.e., changes of the correspondence between the cursor position and joystick movement due to the experimenter's manipulation, which participants were not explicitly told). The probability distribution is updated trial-by-trial with the new incoming performance error. Therefore, there is an estimation of the two types of uncertainties for each trial. A multilevel linear model analysis confirmed the success of the Bayesian modeling showing that participants' behavioral performance was modulated by estimation uncertainty, as well as expectation uncertainty. For example, high levels of estimation uncertainty and expectation uncertainty led to increased reaction times to initiate responses. Interestingly, the post-movement beta rebound amplitude changed in accordance with estimation uncertainty, but not with expected uncertainty, over trials. High amplitudes of beta rebound were associated with low estimation uncertainty. Although beta rebound was also related to performance errors, the authors were able to show that beta rebound was modulated by estimation uncertainty even when performance errors were kept comparable. Based on these findings, the authors concluded that beta rebound indexed the estimation uncertainty about sensory consequences resulting from self-movement.

This study provides a new perspective for understanding beta rebound. However, we wonder whether beta rebound is well positioned for representing estimation uncertainty. From a theoretical point of view, a neural signal and the cognitive activity it represents should occur simul-

taneously. For example, the hypothesis that alpha oscillation is related to the top-down control of visual spatial attention was supported by the finding that alpha power modulation and the attentional control process were detected in a similar post-cue time window (Thut et al., 2006). In the study by Tan et al. (2016), beta rebound emerges after the completion of the movement, which does not seem to be temporally suitable for representing estimation uncertainty related to the forward model. The forward model is active before the actual movement onset and defines the causal relationship between a movement and its resulting sensory consequences and it is used for making predictions (Wolpert and Ghahramani, 2000). Thus, estimation uncertainty can be viewed as the uncertainty of the forward model, which should be represented before the movement offset. The timing of beta rebound is too late for the prediction from the current trial and too early for the prediction from the next trial.

One may argue that based on Bayesian principles, the posterior (i.e., updated estimation) of the current trial is the prior (i.e., estimation before new data) of the next trial. Then beta rebound may represent the next trial's estimation uncertainty indirectly through representing the updated estimation uncertainty in the current trial. This argument is untenable for the following reasons: (1) the updated estimation uncertainty should be represented as a stable state unless it is forced to change, thus it is equally likely to be observed in brain signals at any time, whereas beta rebound is transient; and (2) if beta rebound represents the next trial's estimation uncertainty, we should expect it to show up again in the next trial when the forward model is activated. However, existing evidence shows that the pre-movement beta-power increase and beta rebound are functionally dissociable (Torrecillos et al., 2015).

As an alternative, we suggest that the beta rebound modulation in the task used by Tan et al. (2016) is related to the process of forward model updating. The brain can detect a mismatch between sensory predictions based on the forward model and actual sensory reafference, and this enables an efficient change of the motor plan (Schafer and Marcus, 1973; Behroozmand et al., 2016). At the same time, the outdated forward model needs to be updated (Synofzik et al., 2008). In the task setting used by Tan et al. (2016), the decision about whether the current forward model should be updated should be made after the movement offset when the sensory reafference is processed. This is exactly the time when beta rebound is found. Our hypothesis is consistent with the key finding of Tan et al. (2016), i.e., beta rebound was significantly reduced when there was a sudden change in the correspondence between the controlling movement and the resulting visual feedback (Tan et al., 2014, 2016; Torrecillos et al., 2015). This is also the situation where the forward model requires a substantial updating. Thus, the data seem to suggest that high beta rebound functions to actively keep the existing forward model, whereas low beta rebound is associated with the process of updating the forward model.

Our hypothesis does not conflict with the original finding that beta rebound is correlated with estimation uncertainty. In the task, estimation uncertainty was tightly linked with forward model updating (e.g., low estimation uncertainty requires little forward model updating), so the correlation between beta rebound and estimation uncertainty might be a consequence of the proposed relationship between beta rebound and forward model updating.

Finally, our hypothesis has the potential to reconcile different accounts about the function of beta rebound in the literature (Cassim et al., 2001; Engel and Fries, 2010). On the one hand, our explanation can be seen as an extension of "the status quo" account. Engel and Fries (2010) suggested that in the motor domain, beta oscillation functions to actively maintain the current motor plan. We propose that beta rebound functions to keep the current forward model. This is supported by a recent study showing that primary motor cortex stimulation with transcranial alternating current stimulation at 20 Hz facilitated motor learning and stabilization in a serial reaction time task (Pollok et al., 2015). The 20 Hz stimulation possibly enhanced beta power in the motor cortex and then facilitated the maintenance of the task-related forward model, which is vital in motor control (Wolpert and Ghahramani, 2000). Thus, it led to an enhancement effect on motor learning and stabilization. On the other hand, our explanation provides a new perspective on earlier findings suggesting a role of beta rebound in sensory processing (Cassim et al., 2001; Reyns et al., 2008). Cassim et al. (2001) showed that beta rebound almost disappeared when participants' moving finger was deafferentated by ischemic nerve block. Thus, a role of somatosensory processing was suggested for beta rebound. This classic effect also fits with our proposition that beta rebound maintains the current forward model. When deafferentation was applied to the finger, the participants should experience a drastic prediction error, i.e., no sensory feedback was associated with the finger movement. This would necessarily lead to a change in the forward model of predicting movement-related somatosensory feedback, in which case beta rebound was reduced.

The finding that beta rebound is modulated by the performance in the visuomotor task marks a significant advance in our understanding of beta rebound (Tan et al., 2014, 2016). We suggest that the beta rebound modulation may be best understood as a process related to forward model updating, with high beta rebound relating to the process of actively maintaining the current forward model. Although more evidence is needed to support our proposition and the mechanisms of how beta rebound may be involved in the process remains to be revealed, an interesting prediction from the proposition is that individuals who have difficulties in updating forward model (e.g., cerebellar lesion patients; Synofzik et al., 2008) may have a beta rebound dysfunction.

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