**Q 6**

**Please comment on the Introduction section. Key elements to consider:  
- appropriateness of context  
- purpose of study**

**Reviewer 1** | 03 Oct 2017 | 04:58

**#1**

This is a nice manuscript and reads well. The introduction gives a good overview of the pathways involved in oculomotor control, and describes the motivation of the paper. I have only a few comments.   
  
1) I was a bit surprised that the biomechanical model is all software. My initial expectation was that there was a physical component to it. Maybe that could be clarified.   
2) Line 75: It is unclear what you mean with "simplest" here. Please clarify and modify that sentence.   
3) Line 81: What is meant with 'through channels'. Remember that neurobiologists may read this and may have a very different definition for channels.   
4) Line 98: ...individual SUBsystems...   
5) Line 102: What is meant with physical plants?

**Please comment on the Discussion section. Key elements to consider:  
- adequate discussion of research questions or hypothesis (posed in introduction)  
- conclusions supported by data  
- exhaustive discussion of previously published material (in context to current study)**

**Reviewer 1** | 03 Oct 2017 | 04:58

**#1**

The authors adequately discuss the hypothesis posed, i.e. that closed loop models provide valid tools to test shortcomings in other models. However, they could include a more broader discussion of closed loop models or approaches that are already used.   
Remarks:  
1) Inhibitory feedback. As stated above, please discuss a potential relevance for this feedback in the biological system as well. Is there any evidence it exists?   
2) A more general question that could be addressed is whether inaccuracies in the biomechanical model may introduce errors that propagate through the closed loop system and cannot be counteracted by the nervous system part of the simulation. How can you (or someone using this or related models) exclude introducing (biomechanical) properties that are not present in the biological system, or make sure to not miss critical biomechanical properties that might help remedy some of the shortcomings of the closed loop model?  
3) Would you consider combinations of software models and hardware 'models' part of computational neurobehavior? Considering other brain areas and behaviors outside of oculomotor control, there are quite a few models that combine software and hardware in closed loop conditions, such as robotic arms, or walking machines, which are per definition closed loop. The discussion would benefit from a paragraph that addresses these approaches, and compares to the one you suggest.   
4) Other closed loop approaches: there are several closed loop approaches in biological experiments as well, and the argument here is that closed loop systems develop dynamics that emerge from the fact that the biological circuits receive instantaneous (closed loop) feedback. Typically, the 'brain' here is the biological part, and the sensory feedback is provided by an external apparatus that provides the appropriate feedback in real time. Closed loop systems have been used to study, for example, fly vision, but also other behaviors. In the example of the fly, the visual environment is moved in realtime to provide adequate feedback for saccade like behaviors. The discussion would benefit from a section that introduces the arguments behind closed loop approaches in general (vs open loop), from which you could then move towards your own closed loop model approach, and its benefits over others.

**Q 7**

**Please comment on the Material and Methods section. Key elements to consider:  
- objective errors  
- correct choice of methods  
- comprehensive description of methods  
- accuracy of procedures  
- quality of figures and tables**

**Reviewer 2** | 17 Oct 2017 | 10:59

**#1**

1. Although I understand that the major scope of the paper is to integrate the previous work (Cope et. al. 2017) with a saccadic burst generator model and biomechanical model of the eye, the BG modeling part of the work has to be explained or atleast added as an Appendix to the enhance understanding of the model. Additionally the Cope et al. 2017 paper cited is from the archive and relevant parts of it must be presented in the current work to aid the review process.  
  
2. It would be further useful if the information flow in the model is explained in a paragraph from how stimulus enters into the model, passes through different layers and how the loop ends.  
  
3. Are the weights wact, wsh and wmn trained in the model, if so how and if they have been assigned how are they chosen?   
  
4. The role of the dopamine parameter d which modulates input activation to D1 and D2 MSNs is not clear in the model. How does it control of switching between the pathways and dynamics in the BG? Furthermore the authors have not considered the conventional prediction error notion of dopamine and its plasticity effects in the striatum and this has to be substantiated.  
  
5. The idea the weight connectivity from the deep SC to the SBG is implemented by the widening projection field is not clear for the reader. The authors mention in lines 406-407 “This led us to hypothesize that the retinotopic mapping be accompanied by an associated widening projection field such that the hill of activity in superior colliculus is invariant with position on the collicular surface”. What is the collicular surface here and given the fact that the activity is large in the SC for stimuli closer to the fovea shouldn’t the connectivity be convergent? This part is very confusing and needs further explanation.   
  
6. In Eq 26 describing the channel weight connectivity from SC\_deep to the SBG, the use of the exponential and the sine function seems to account for the magnification in the SC as the activity in the SBG will exponentially increase with increasing eccentricities this maintaining the invariant property. So why was there a need for a widening projection field in the previous layer?   
  
7. The activity coming into SC\_deep is from both the FEF and the SC\_sup layers, both having a Gaussian projection. It is not clear what information do both these areas bring into the SC\_deep layer and how this contributes to the building up of target luminescence in this layer.  
  
8. The description of the biomechanical eye is insufficient. Firstly what type of the dynamics of the muscle models were used for the EOMs and what input from the SBG was fed into these muscles has to be clarified. 

RESPONSE:

The proposed implementation of the biomechanical eye includes modeling and simulation of two types of muscle models of different complexity.

The first models muscles using linear path actuators. This simplistic model of ideal muscles can be easily integrated with high level brain models. Muscle wrapping around the eye can be supported while in the proposed implementation we also include in the simplistic model passive forces that stem from the mechanical interaction of the eye globe and the surrounding soft tissues.

The more complex model supported is a modification of the Thelen model [] that is also supported by OpenSim and is based on a Hill-type model. It includes realistic muscle wrapping geometric entities of the muscle fibers, while it accommodates for both activation and contraction dynamics.

Based on the above and also considering that the research question to be addressed is not directly affected by the muscle dynamics (SEB I THINK YOU CAN ADD HERE MORE STUFF) we used the simplistic muscle models to extract the experimental results presented in Section XXX.

Moreover the SBG… (THIS IS ALSO FOR YOU…)

In the revised version of the manuscript section 2.4 has been updated so as to include more information on the biomechanical eye model and to include the above discussion.

9. The authors say that the rotational state of the eye is used to compute the eye’s frame of reference for feedback, but this suggests that take of granted that the rotational state is available for the brain for computation. The way to estimate the rotation state would be to use the state of the EOMs (for example the length of the muscles which could be sensed by some proprioceptive receptors) to map to the eye’s reference frame.  
  
10. A simple schematic of the biomechanical eye and the screen, describing their position and orientation in the Cartesian space, along with the luminescent targets would be good to enhance understanding.

RESPONSE:

Section 2.4 has been updated including several schematics of the biomechanical eye so as to ease understanding of the geometric virtual setup.