Reply to Bram Zandbelt

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Redirect task and compensation functions

It is well known that both countermanding and redirect tasks engage elements of proactive and online control that facilitate performance (Chikazoe et al., 2009; Chen et al., 2010; Stuphorn et al., 2010; Zandbelt and Vink, 2010). Because the primary goal of this paper was to study the nature of online control, we set a deadline of 400 ms so that proactive control, which tends to slow down saccades subsequent to a redirect trial, was not the primary element dominating performance. However, one consequence of imposing such a deadline is that monkeys might have been pushed to plan the first saccade, ignoring the final target in some cases, which may have resulted in more errors overall. Increase in errors may also be due to a failure in triggering the online control process in a fraction of trials. However, by assuming that the lower asymptote of the compensation function represents the proportion of trials that did not engage online control, these components were factored out in a conservative way (Logan, 1994; Ramakrishnan et al., 2010). The compensation function that was used for subsequent modeling is only reflective of elements that should be engaged during online control and thus it justifies our rationale for testing subsequent race models. The evidence of online control is clearly seen in the time course of the saccade deviation profile in microstimulated step trials (See Fig 4B in Ramakrishnan et al., 2012), which strongly resembles the pattern of neural activation seen in single-unit data from movement cells in the FEF of monkeys performing the countermanding and double-step tasks (Hanes, 1998; Murthy et al., 2009).

Modeling the stimulation evoked saccade deviation profile

Although the GO-GO+STOP (GGS) was on average the better model, we do not reject the other competing models, which on certain sessions were able to outperform the GGS model (in the least squares sense). As stated in the discussion, we could have performed a formal comparison by fitting simultaneously both the behavioral data and the deviation profile. We avoided it for the following reasons. First, we were simulating psychological models that have traditionally been used to fit behavioral data, so our approach was aimed at testing the applicability of these
models to the deviation data. Second, if one fits the behavioral data as well as the deviation profiles, the models may be less accurately fit to the former, which we felt was undesirable.

As stated by the Journal Club author, the variability across sessions may reflect monkeys using different strategies/mechanisms. However, a more parsimonious explanation for this variability might be that monkeys have been able to modulate the $\beta_{GO2}$ parameter that constitutes the basic GGS model such that on some sessions (or even trials) monkeys implemented a selective STOP (that is engaged in parallel with GO2; $\beta_{GO2}=0$), while on others sessions they implemented a global STOP signal ($\beta_{GO2}=1$). By this reasoning, the intGS models (GGS and GSG) are a better fit on 29/43 sessions as compared with the GG-aDiff model (or the GG-a) with different rates for GO1 and GO2, which interestingly, also has more free parameters than the intGS models.

As stated earlier, the intention of the analyses was not to explicitly attempt to fit the deviation profile, but rather to try to predict it based on the compensation function. Nevertheless we believe this fit may be improved by several means. First, by considering possible nonlinearities in the interaction between microstimulation and the saccade being planned. Second, by factoring the effect of the attention and error correction on the GO2 process, which would also affect the deviation profile. This notwithstanding, from the perspective of this paper we feel it is most relevant to be able to predict the change of deviation from the initial direction to the crossover time, as this epoch would be most reflective of the nature of online control, rather than predicting the extent of the later part of the deviation due to the GO2 process per se. In this respect, the significant correlations we observe between the predicted and observed crossover time, the target step reaction time (TSRT; a measure of control derived from the race model; see fig. 8 and discussion) justifies the rationale to our approach.

**Modeling the RTs**

Although the saccade RTs to the first target were well predicted in only 29/43 sessions, this is a comparison made by grouping the RTs of different TSDs. However, considering the variability in RTs across TSDs, when RTs were compared at every
TSD individually, the RTs for the longer TSDs were predicted in 39/43 sessions (t-test: \( p > 0.05 \)). The discrepancy between predictions of the race model, particularly at the shorter TSD’s has also been reported by others (Colonius, 2001; Boucher et al., 2007; Ramakrishnan et al., 2010).

One obvious way to resolve the discrepancy between the observed and predicted GO2 RTs is to model GO1 and GO2 with different rates. The GG-aDiff model was in fact motivated to test this idea. However, although the predictions of the GO2 RT improved the fit to the RT data (see fig. 7D in Ramakrishnan et al., 2012), the deviation profile did not improve from the basic GG-a model, despite the addition of another parameter. For this reason, we did not model a second GO2 process when considering the GO-STOP models. The addition of the GO2 parameter would have perhaps only improved on the fits, but with the cost of using another parameter, which we felt was undesirable.

References


