Reply to Maslovat et al.

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REPLY: We welcome Maslovat et al.’s (2015) recent replication of results and their comments in the Letter to the Editor (doi:10.1152/jn.00154.2015) on work we previously reported (Marinovic et al. 2013). We originally interpreted the pattern of premotor reaction time (RT) data obtained in our study (and reproduced by Maslovat et al. 2015) as evidence that response-related activation increases gradually in anticipation of a visual imperative stimulus (IS) and that the increase continues up to the moment of response initiation. This was evident in an increased shortening of premotor RTs as a function of a shorter gap between the presentation of loud auditory stimulus (LAS) and the IS. However, in their Letter to the Editor, Maslovat et al. (2015) provide a new analysis indicating that there is no gradual increase when a true startle reflex response is evoked by the LAS [as indexed by sternocleidomastoid (SCM) activation]. Their evidence is that on trials when SCM was activated in response to the LAS, there was no statistically significant effect of the time of LAS delivery on premotor RT. They conclude that neural excitability during movement preparation reaches an asymptote well in advance of IS presentation and suggest that our original interpretation of the results was mistaken and arose because we failed to differentiate between trials in which the SCM was activated (SCM+ trials) and those in which it was not (SCM− trials). They further note that a constant level of preparatory activity prior to response initiation is supported by the results of Carlsen and MacKinnon (2010), who found evidence that responses were well prepared 500 ms before the IS onset (although in different conditions to those tested by Marinovic et al. 2013 and Maslovat et al. 2015).

Though this criticism deserves consideration, we will raise a few points that we believe are worthy of attention for the continuing development of the field.

In Marinovic et al. (2013) we considered two types of model: one in which preparatory activity was constant over the period preceding response initiation (like that favored by Maslovat et al. 2015) and one in which preparatory activity was monotonically increasing up to the moment of response initiation. For each type, we considered that the response could be triggered either by the IS or by the LAS and derived predictions for the pattern of premotor RTs obtained in the experiments assuming one or the other type of triggering, given the four possible models. We found that only the model in which preparatory activation was increasing up to response initiation and the response was triggered by the LAS reproduced the pattern of results obtained in our experiment (and reproduced by Maslovat et al. 2015). Maslovat et al.’s interpretation is quite different: preparatory activation is constant over the period prior to response initiation, and when the startle reflex is evoked (SCM+ trials), the response is triggered by the LAS; when the startle reflex is not evoked (SCM− trials), the response is triggered by the IS. They suggest, therefore, that the pattern of data reported in Marinovic et al. (2013) does not reflect on an increasing level of preparatory activation, but on the combination of trials in which responses were triggered by the LAS and trials in which responses were triggered by the IS.

The SCM+ trial results described by Maslovat et al. (2015) are indeed consistent with constant preparatory activity: we showed that when the response is triggered by the LAS and the preparatory activity is constant, then the premotor RT (referenced to the LAS presentation time) does not vary with the LAS presentation time (Marinovic et al. 2013, Fig. 8D). However, the data from the SCM− trials reported by Maslovat et al. (2015) do not show the pattern predicted by constant activation models or by IS triggering; rather, they appear to retain the pattern predicted by the increasing preparatory activation model with LAS triggering (Marinovic et al. 2013; Fig. 9B).

Thus the data reported by Maslovat et al. (2015) would seem to present a problem: the SCM+ data are consistent with constant preparatory activity and LAS triggering, whereas the SCM− data are consistent with increasing preparatory activity and LAS triggering. One straightforward way to resolve this discrepancy is to suppose that the moment at which peak preparatory activity is reached varies from trial to trial: on some trials it occurs in advance of the moment that the response is initiated (and remains constant up until that moment), whereas on others it is still increasing when the response is initiated. If we then propose that SCM activity is correlated with a high level of preparatory activity, we would predict that the SCM+ trials would tend to be those during which preparatory activity reached its maximum level somewhat early. This simple hypothesis can explain the pattern of data obtained in both experiments, why SCM+ trials are consistent with a constant level of preparatory activity and why SCM− trials are consistent with increasing activity, and there is no need to propose any mixed triggering model in which either the IS or the LAS could be responsible for triggering.

The account given above differs from that offered by Maslovat et al. (2015) in two ways. First, responses in SCM+ and SCM− trials are not triggered by different stimuli. Second, SCM activation is not a requirement for triggering by the LAS; it is simply an indicator of reflex excitability at the time of LAS delivery, excitability that is greater when the level of preparatory activity is greater. Maslovat et al. (2015) suggest instead that when the startle reflex is evoked, the “voluntary” response
is triggered by the LAS (rather than the IS) via a different, subcortical pathway. Triggering via this subcortical pathway is quicker than triggering by the normal (cortical) route, which accounts for the unusually short RTs often observed when a LAS is presented. According to this hypothesis, elicitation of a true startle response by the LAS is essential for early triggering. It is worth noting, therefore, that in the Maslovat et al. (2015) study, there are SCM+ trials with RTs that were much longer than one would expect (>160 ms) while at the same time there were SCM− trials with much shorter RTs than expected (<80 ms). Thus it is possible to have fast reactions without SCM activation, and vice versa (see Fig. 4 in Maslovat et al. 2015). As pointed out by Maslovat and colleagues in the Letter to the Editor (doi:10.1152/jn.00123.2015), earlier responses triggered by loud noises do not require the observation of SCM activation. In other words, you can extinguish the reflex and still have earlier than normal responses (Maslovat et al. 2012; Valls-Solé et al. 2005). They make the claim that these are a few specific cases (e.g., prepulse inhibition); however, their own results are unambiguous in that the reflex is not necessarily coupled with early responses even under nonspecific cases.

REFERENCES
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