Journal Club

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Neurally Constrained Cognitive Modeling Clarifies How Action Plans Are Changed

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Review of Ramakrishnan et al.

Cognitive neuroscience aims to explain how cognitive functions arise from brain processes using computational models to describe the mapping between behavioral and neural data. This approach has previously been used to understand the neural mechanisms of stopping an action. A paper recently published in *The Journal of Neuroscience* applies this method to explain how actions are changed.

Stopping has typically been investigated with a task in which subjects are asked to respond to go-signals, but to stop their response when a stop-signal follows the go-signal. Stopping is easy when the stop-signal is presented early during action preparation (<100 ms after the go-signal), but becomes increasingly difficult when preparation gets closer to completion (>200–300 ms after the go-signal), a relationship referred to as the inhibition function. The precise time of the inhibition function varies with natural response times and task demands. Furthermore, responses that escape inhibition are faster than the average response. These behavioral characteristics can be explained by a model that describes performance as the outcome of a race between a GO process and a STOP process that have independent random finish times (Logan and Cowan, 1984). However, accounting for both behavioral and neural data requires an interactive race model, in which STOP interrupts GO (Boucher et al., 2007).

Changing actions closely resembles stopping (Logan and Burkell, 1986; Camalier et al., 2007). In the double-step eye-movement change task, subjects are asked to make a saccade to peripheral targets, but to redirect gaze when the target changes position. Change performance has the characteristics of a race: the probability of compensating for the change in position decreases with the delay between the initial onset of the target and when it moves, as described by the compensation function. Moreover, saccades that could not be redirected are faster than average; however, it is unclear which processes compete and how they interact. Is the race a direct competition between the processes producing the responses to the initial target (GO1) and final target (GO2) or is an additional STOP process involved? Additionally, when and how do these processes interact?

These questions were recently addressed in a study by Ramakrishnan et al. (2012). Monkeys were trained to perform a modified double-step task. To measure the time course of the changing saccade plan, the authors used microstimulation of the frontal eye fields to evoke saccades at various times after the change-signal. This resulted in a profile of saccade deviation showing that saccades evoked earlier deviated toward the initial target, whereas saccades evoked later deviated toward the final target. The time at which the deviation crossed over from the initial to the final target (crossover time) was taken as an estimate of the time when the response changed.

To identify the mechanism underlying change performance, Ramakrishnan et al. (2012) compared race models that differed in two dimensions: the number of processes and the manner of interaction. First, GO-GO models assumed a race between GO1 and GO2, whereas GO-STOP models assumed a race between GO1 and STOP, with GO2 running in parallel. Second, GO1 and GO2/STOP could race independently without interacting, interact nonselectively (both GO1 and GO2 are inhibited), or interact selectively (GO1 is inhibited, GO2 continues in parallel). Models were fitted to the behavioral data and best-fitting parameters were used to simulate saccade deviation profiles.

The results showed that a model in which GO1 and GO2 interacted nonselectively and models in which GO1 and GO2/STOP did not interact predicted compensation functions with higher error rates than observed or produced saccade deviation profiles failing to cross over. Better fits were obtained with a model in which GO1 and GO2 were nonselectively inhibited by a STOP process and models assuming selective inhibition of GO1.

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These models accounted equally well for the behavioral data, but the selective GO-STOP model predicted crossover times most accurately. Overall, selective GO-STOP was the best-fitting model in almost half of all sessions, whereas selective GO-GO and nonselective GO-STOP were better models in a third and a quarter of the sessions, respectively. It was concluded that changing actions requires a STOP process that selectively inhibits the response to the initial target, while allowing the response to the final target to continue in parallel. Ramakrishnan et al. (2012) further argued that a nonselective inhibitory mechanism coexists and that selective and nonselective mechanisms may represent different performance strategies.

Ramakrishnan et al. (2012) clearly ruled out models in which the processes do not interact, but their results are less conclusive about which of the interactive race models accounted best for performance. Actually, the similarities are more striking than the differences and it is unclear whether any model would have outperformed the others had a formal statistical model comparison been performed. Furthermore, none of the models fitted the data perfectly: response time (RT) distributions could not be fitted in up to half of all sessions and the discrepancy between the predicted and observed saccade deviation profiles was half the size of the observed span. As discussed below, these imperfect fits might be explained by atypical performance, potential shortcomings in measurements and models, and differences in performance strategies across sessions.

The compensation functions suggest that task performance may not have been in accordance with a race in all sessions. In this task, the lower asymptote of the compensation function is typically near 0% error probability, indicating that when the initial and final targets are displayed in immediate succession, the saccade can be successfully changed. In contrast, the reported error probability was on average ~30% (and in some sessions even 70%). This is characteristic of a strategy in which, on a certain proportion of trials, subjects respond to the initial target regardless of whether the final target is presented (Logan and Cowan, 1984). Why would the monkeys adopt such a strategy? Perhaps the imposed response deadline of 400 ms encouraged them to trade accuracy on change trials for speed on no-change trials. From the monkey's perspective, this was not a bad strategy, because it yielded reward in 80% of all trials.

It is also possible that measurements and model architectures have been incorrect or incomplete descriptions of the underlying processes. The crossover time measured from the saccade deviation profiles was decisive in selecting the best-fitting model, but may actually reflect the time when GO1 and GO2 are counterbalanced rather than the time when the response changes. Moreover, all models assumed that GO1, GO2, and STOP run in parallel. Although there is no doubt that GO1 and STOP run in parallel (Logan and Burkell, 1986), STOP and GO2 may occur serially (Verbruggen et al., 2008, but see Camalier et al., 2007). Another assumption was that GO1 and GO2 receive driving input of equal strength. However, this is contrary to a common finding in change tasks that change RTs (resulting from GO2) are faster than no-change RTs (resulting from GO1) (Logan and Burkell, 1986; Camalier et al., 2007; Shankar et al., 2011) and could explain why models, at least in the example session, overestimated change RTs.

As Ramakrishnan et al. (2012) suggest, models could represent different performance strategies and these may have differed between sessions. At first, this seems unlikely; why would strategies differ across sessions even though the tasks were identical? Notably, the data were obtained from two subjects who may have used different strategies. Indeed, the best-fitting model parameters show considerable variability between them. Performance strategies probably not only differ between subjects but also depend on task design. For example, it has been argued that a selective stopping strategy is optimal when stop-signals are frequent and anticipated, whereas a nonselective stopping strategy is useful when stop-signals are infrequent and unpredictable (Aron, 2011). It is possible that selective GO-STOP was the best model in this study because change trials occurred frequently and the response to be stopped was entirely predictable. These insights highlight that actions may be changed in multiple ways and that there may be no one-to-one mapping between neural mechanisms and cognitive functions.

To further elucidate the various mechanisms by which actions are changed it would be useful to extend the approach used by Ramakrishnan et al. (2012). Future studies should compare race models with parallel and serial architectures, preferably on measures that are sensitive to STOP-GO2 processing architecture, such as the relation between reprocessing time and intersaccadic interval (Ray et al., 2004), the relation between change RT and stop-change delay (Verbruggen et al., 2008), or corrective RT (Camalier et al., 2007). Furthermore, the selective GO-STOP model needs specification: it is assumed that the STOP process "knows" which GO process should be inhibited, but it is not explained. Alternatively, the STOP process might inhibit all GO processes nonselectively and then selectively reinitiate GO2. Finally, it will be important to examine whether the mechanism for changing eye movements in monkeys extends to humans and hand movements, for instance, with single-pulse transcranial magnetic stimulation over the left and right M1 in humans to track the time course of corticospinal excitability related to performance in a bimanual change task.

In summary, Ramakrishnan et al. (2012) used the powerful concept of neurally constrained cognitive modeling to reveal how action plans are changed. They have provided a valuable starting point for future studies to extend and refine these models that ultimately will help in understanding the neural mechanisms of decision-making and executive control.

References

Aron AR (2011) From reactive to proactive and selective control: developing a richer model for stopping inappropriate responses. Biol Psychiatry 69:e55–e68.

Boucher L, Palmeri TJ, Logan GD, Schall JD (2007) Inhibitory control in mind and brain: an interactive race model of countermanding saccades. Psychol Rev 114:376–397.

Camalier CR, Gotler A, Murthy A, Thompson KG, Logan GD, Palmeri TJ, Schall JD (2007) Dynamics of saccade target selection: race model analysis of double step and search step saccade production in human and macaque. Vision Res 47:2187–2211.

Logan GD, Burkell J (1986) Dependence and independence in responding to double stimulation: a comparison of stop, change, and dual-task paradigms. J Exp Psychol Hum Percept Perform 12:549–563.

Logan GD, Cowan WB (1984) On the ability to inhibit thought and action: a theory of an act of control. Psychol Rev 91:295–327.

Ramakrishnan A, Sureshbabu R, Murthy A (2012) Understanding how the brain changes its mind: microstimulation in the macaque frontal eye field reveals how saccade plans are changed. J Neurosci 32:4457–4472.

Ray S, Schall JD, Murthy A (2004) Programming of double-step saccade sequences: modulation by cognitive control. Vision Res 44:2707–2718.

Shankar S, Massoglia DP, Zhu D, Costello MG, Stanford TR, Salinas E (2011) Tracking the temporal evolution of a perceptual judgment using a compelled-response task. J Neurosci 31:8406–8421.

Verbruggen F, Schneider DW, Logan GD (2008) How to stop and change a response: the role of goal activation in multitasking. J Exp Psychol Hum Percept Perform 34:1212–1228.