

Rapid Feedback Responses Arise From Precomputed Gains

David W. Franklin

Technical University of Munich

To reach for an object, the sensorimotor control system must estimate the location of both the hand and object. Using this information along with the configuration of the limb, the sensorimotor control system can determine the appropriate set of motor commands that will bring the hand to the target. This is true regardless of whether the movement is a full reaching movement to the target or simply a corrective response to a shift in the object's location. While movement initiation takes 150 ms (from a visual signal to muscle activity; Pascual-Leone et al., 1992), movement correction to shifts in the target, hand position or background take 100 ms (to muscle activity; Franklin and Wolpert, 2008; Pruszynski et al., 2010; Franklin et al., 2014), a difference of 50 ms.

In this issue, Smeets and colleagues argue that the difference in the latency between initiating a movement and initiating a corrective response to a visual perturbation is due to the absence of the detection stage suggested by Donders (Donders, 1969). Specifically, they suggest that rapid visuomotor responses to shifts in the target location do not require the sensorimotor control system to detect the shift, whereas initiating a movement requires detection of a change in the environment before the movement can be initiated. While not all movements need to be made to a change in the environment, a movement is usually initiated to either a change in the world, a decision process leading to the movement, or both, all requiring further processing time. While broadly consistent with the viewpoint of Smeets and colleagues, I suggest that these differences in latencies may arise from differences between having to compute feedback gains before the start of a movement and utilizing prespecified feedback gains as would normally occur within in a movement.

The proposal that these rapid corrective responses do not require a specific change detection stage is broadly consistent with the theory of optimal feedback control (Todorov and Jordan, 2002; Scott, 2004; Todorov, 2004; Guigon et al., 2007). Optimal feedback control (OFC) suggests that the process of motor control involves the prior calculation of a series of feedback gains to produce a movement for which the expected loss (or cost) is minimized. Specifically, OFC finds the optimal feedback control law that, subject to the noise and task demands, minimizes

The author was with the Computational and Biological Learning Laboratory, Dept. of Engineering, University of Cambridge, Cambridge, UK, at the time of research. The author is now with the Dept. of Sport and Health Sciences, Technical University of Munich, Munich, Germany. Please address author correspondence to David W. Franklin at david.franklin@tum.de.

a cost function compromised by accuracy and energetics. As the feedback gains are optimized to minimize cost, they will only correct for task-relevant errors. This means that the errors can continue to build up in dimensions of the movement that are irrelevant, but will be rapidly corrected in dimensions that contribute to task success. Indeed, large differences in the visuomotor feedback gains have been seen between task-relevant and task-irrelevant conditions (Franklin and Wolpert, 2008; Knill et al., 2011; Franklin et al., 2014). More critically, these feedback gains act continuously throughout the movement, with time varying patterns throughout the movement (Liu and Todorov, 2007; Dimitriou et al., 2013) (see similar patterns of responses in Oostwoud Wijdenes et al., 2011). This is particularly relevant as, if the feedback gains are operating continuously, they operate regardless of a disturbance in the hand or target. That is they do not require a specific change detection stage just as suggested by Smeets and colleagues. Moreover, we would expect these feedback responses to operate even if the visual disturbance was within the natural variability of movements, as shown for stretch reflex responses (Crevecoeur et al., 2012).

Smeets and colleagues outlined two distinct findings in terms of the response times to shifts in the visual environment. For most of the studies a rapid response occurred (<150 ms) (Brenner and Smeets, 2003; Saunders and Knill, 2004; Saijo et al., 2005) whereas for a few studies the responses were much later (>200ms) (Boulinguez and Nougier, 1999). They explain the late response as a result of experiments in which the same target is not simply moved, but that one target is extinguished while another one is illuminated in a darkened room. In these studies they suggest the subjects need to detect the new target, as the original target may still be visible. The extensive delay in the response may not simply be a problem of requiring detection of the new target, but if the original target remains visible at all, then the sensorimotor control system may keep the feedback gains set to the original target. In this case, the corrective response to the disturbance may occur only at a voluntary latency, possibly involving a different neural circuit. Alternately, if the original target remains visible (either through visual persistence or through scattered light), the feedback gain may initially be set relative to the original target, only slowly shifting to the newly illuminated target. This could then use the same neural circuitry but may explain a delay in the response. While many studies have shown similar patterns of responses for both target perturbations and cursor perturbations, a recent study has suggested that they have different neural pathways, as the target corrective responses are influenced by attentional demands, whereas the cursor responses are independent of attention, instead relying on a visuomotor binding mechanism (Reichenbach et al., 2014). Together these two mechanisms are used to associate the appropriate visual information to the hand or the target and limit feedback responses to distractors. This linking of specific visual information with the target or hand may also explain the delay in shifting these gains to a newly visible target, as additional mechanisms (attention or visuomotor binding) would be necessary to shift the feedback to the appropriate target.

It has been shown that these rapid visuomotor feedback responses are insensitive to the number of possible responses (Reynolds and Day, 2012) unlike voluntary movements in which the reaction time varies with the number of alternative movements (Hick, 1952). Despite the fact that the required feedback responses are almost never known in advance—the perturbations or errors could occur in any direction and with any extent the response time of the corrections is consistently

faster than the simple response time of a known target where the motor plan can be prepared ahead of time. This rapid response and absence of choice-dependent response time has been suggested to indicate a direct subcortical pathway through the superior coliculus (Reynolds and Day, 2012). However, this does not necessarily indicate a subcortical pathway, but rather that the sensorimotor control system has prepared the feedback gains ahead of time. In this case the sensorimotor control system simply unveils, in real time, the feedback gains for the movement. The few exceptions would involve conditions in which the prepared feedback gains do not correct optimally for the imposed changes (e.g., combined cursor perturbation and task change (Dimitriou et al., 2013) or rotations of grasp points (Voudouris et al., 2013). In these conditions the initial feedback response is still rapid but not necessarily appropriate for the task. Instead the later response, (~160ms; Voudouris et al., 2013) shows the appropriate task-relevant correction. This extra computational time may arise from recomputation of the feedback gains. These later modified feedback gains behave similarly to model predictive control (Lee, 2011) in which the feedback gains are continually recomputed as the movement progresses (Dimitriou et al., 2013). However the extra temporal delay in expressing the recomputed gains for more complex errors or task-changes suggests that this recomputation takes more time than that allowed for the fastest visuomotor feedback responses.

My suggestion that the absence of a response selection—delay relationship indicates preprepared feedback gains does not necessarily argue against a subcortical pathway as proposed (Reynolds and Day, 2012). However, the onset time of long latency stretch reflex responses do not follow Hicks law (Pruszynski et al., 2008) and have been shown to have a cortical component (Pruszynski et al., 2011). If the rapid visuomotor responses either contain a cortical component (or are cortical in nature), this could explain the extensive evidence that such responses exhibit complex patterns of task-dependent modulation (Franklin et al., 2008; Knill et al., 2011; Franklin et al., 2012; 2014). Importantly, it has been shown that only the long latency stretch reflex responses provide the appropriate responses depending on the limb dynamics (Kurtzer et al., 2008; 2009) and that this specific component is cortical in nature (Pruszynski et al., 2011). Unlike stretch reflexes, in which the proprioception arises from the stretched muscles and often (but not always) signals the appropriate corrective response, visuomotor responses have no labeled lines that might suggest the appropriate combination of muscles for the responses. Instead the sensorimotor control system must combine the visual signal about required correction in retinal space with information about the intrinsic configuration of the effector. As the sensory information about the current limb configuration is delayed and would produce inappropriate corrective movements to the target (Miall et al., 2007), the rapid visuomotor corrective responses must combine the sensory information with predictive state estimation (for a review see Franklin and Wolpert, 2011) to compensate for the neuro-mechanical properties of the limb (Gritsenko et al., 2009). If this rapid visuomotor response is due to a dedicated subcortical pathway, then it must also receive connections from cortical and cerebellar structures that respectively provide task-dependent and limb configuration dependent (state estimation) information for the appropriate corrections.

One important characteristic of these rapid visuomotor responses is that the feedback gain appears to be zero when the arm is stationary or performing a relatively isometric task. To examine the time course of the visuomotor gains to

perturbations of the visual hand position, Dimitriou et al., (Dimitriou et al., 2013) applied perturbations at seven different points throughout the movement. When the perturbation occurred at the end of the movement, the response magnitude was initially close to zero—increasing primarily after 230 ms (see Figure 2 of Dimitriou et al., 2013). A similar finding (unpublished) was found in a stationary bimanual bar manipulation task as described in (Dimitriou et al., 2012). When no movement is occurring, the responses, if present, occur at greater than 230 ms. Thus these responses are distinct from those of saccades, (which can be elicited at any moment in time) in that they only exist during movements. This suggests that they require either a descending signal allowing them to take place (e.g., uninhibition) or require a process that sets up their appropriate gain for the task.

Smeets and colleagues have suggested that the rapid visuomotor feedback responses are rapid compared with simple reaction time tasks because they lack the change detection phase of Donders (Donders, 1969). I suggest that the reason that this detection phase is unnecessary is that the sensorimotor control system has, before the movement, set up the appropriate feedback gains to act throughout the movement. Moreover, it has done so through prior binding of the visual signal of the cursor or target through visuomotor binding or attention respectively (Reichenbach et al., 2014) to limit the effects of distractors. The current evidence for the modulation and control of these visuomotor responses suggests a control process similar to optimal feedback control.

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References

- Boulinguez, P., & Nougier, V. (1999). Control of goal-directed movements: the contribution of orienting of visual attention and motor preparation. *Acta Psychologica*, *103*, 21–45. [PubMed doi:10.1016/S0001-6918\(99\)00022-0](#)
- Brenner, E., & Smeets, J.B.J. (2003). Fast corrections of movements with a computer mouse. *Spatial Vision*, *16*, 365–376. [PubMed doi:10.1163/156856803322467581](#)
- Crevecoeur, F., Kurtzer, I., & Scott, S.H. (2012). Fast corrective responses are evoked by perturbations approaching the natural variability of posture and movement tasks. *Journal of Neurophysiology*, *107*, 2821–2832. [PubMed doi:10.1152/jn.00849.2011](#)
- Dimitriou, M., Franklin, D.W., & Wolpert, D.M. (2012). Task-dependent coordination of rapid bimanual motor responses. *Journal of Neurophysiology*, *107*, 890–901. [PubMed doi:10.1152/jn.00787.2011](#)
- Dimitriou, M., Wolpert, D.M., & Franklin, D.W. (2013). The Temporal Evolution of Feedback Gains Rapidly Update to Task Demands. *The Journal of Neuroscience*, *33*, 10898–10909. [PubMed doi:10.1523/JNEUROSCI.5669-12.2013](#)
- Donders, F.C. (1969). On the speed of mental processes. *Acta Psychologica*, *30*, 412–431. [PubMed doi:10.1016/0001-6918\(69\)90065-1](#)
- Franklin, D.W., Burdet, E., Tee, K.P., Osu, R., Chew, C.-M., Milner, T.E., & Kawato, M. (2008). CNS learns stable, accurate, and efficient movements using a simple algorithm. *The Journal of Neuroscience*, *28*, 11165–11173. [PubMed doi:10.1523/JNEUROSCI.3099-08.2008](#)
- Franklin, D.W., Franklin, S., & Wolpert, D.M. (2014). Fractionation of the visuomotor feedback response to directions of movement and perturbation. *Journal of Neurophysiology*, *112*, 2218–2233. [PubMed doi:10.1152/jn.00377.2013](#)

- Franklin, D.W., & Wolpert, D.M. (2008). Specificity of reflex adaptation for task-relevant variability. *The Journal of Neuroscience*, 28, 14165–14175. [PubMed doi:10.1523/JNEUROSCI.4406-08.2008](#)
- Franklin, D.W., & Wolpert, D.M. (2011). Computational mechanisms of sensorimotor control. *Neuron*, 72, 425–442. [PubMed doi:10.1016/j.neuron.2011.10.006](#)
- Franklin, S., Wolpert, D.M., & Franklin, D.W. (2012). Visuomotor feedback gains upregulate during the learning of novel dynamics. *Journal of Neurophysiology*, 108, 467–478. [PubMed doi:10.1152/jn.01123.2011](#)
- Gritsenko, V., Yakovenko, S., & Kalaska, J.F. (2009). Integration of Predictive Feedforward and Sensory Feedback Signals for Online Control of Visually Guided Movement. *Journal of Neurophysiology*, 102, 914–930. [PubMed doi:10.1152/jn.91324.2008](#)
- Guigon, E., Baraduc, P., & Desmurget, M. (2007). Computational motor control: redundancy and invariance. *Journal of Neurophysiology*, 97, 331–347. [PubMed doi:10.1152/jn.00290.2006](#)
- Hick, W.E. (1952). On the rate of gain of information. *The Quarterly Journal of Experimental Psychology*, 4, 11–26. [doi:10.1080/17470215208416600](#)
- Knill, D.C., Bondada, A., & Chhabra, M. (2011). Flexible, task-dependent use of sensory feedback to control hand movements. *The Journal of Neuroscience*, 31, 1219–1237. [PubMed doi:10.1523/JNEUROSCI.3522-09.2011](#)
- Kurtzer, I., Pruszynski, J.A., & Scott, S.H. (2009). Long-latency responses during reaching account for the mechanical interaction between the shoulder and elbow joints. *Journal of Neurophysiology*, 102, 3004–3015. [PubMed doi:10.1152/jn.00453.2009](#)
- Kurtzer, I.L., Pruszynski, J.A., & Scott, S.H. (2008). Long-latency reflexes of the human arm reflect an internal model of limb dynamics. *Current Biology*, 18, 449–453. [PubMed doi:10.1016/j.cub.2008.02.053](#)
- Lee, J.H. (2011). Model predictive control: Review of the three decades of development. *International Journal of Control, Automation, and Systems*, 9, 415–424. [doi:10.1007/s12555-011-0300-6](#)
- Liu, D., & Todorov, E. (2007). Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *The Journal of Neuroscience*, 27, 9354–9368. [PubMed doi:10.1523/JNEUROSCI.1110-06.2007](#)
- Miall, R.C., Christensen, L.O.D., Cain, O., & Stanley, J. (2007). Disruption of state estimation in the human lateral cerebellum. *PLoS Biology*, 5, e316. [PubMed doi:10.1371/journal.pbio.0050316](#)
- Oostwoud Wijdenes, L., Brenner, E., & Smeets, J.B.J. (2011). Fast and fine-tuned corrections when the target of a hand movement is displaced. *Experimental Brain Research*, 214, 453–462. [PubMed doi:10.1007/s00221-011-2843-4](#)
- Pascual-Leone, A., Valls-Solé, J., Wassermann, E.M., Brasil-Neto, J., Cohen, L.G., & Hallett, M. (1992). Effects of focal transcranial magnetic stimulation on simple reaction time to acoustic, visual and somatosensory stimuli. *Brain*, 115(Pt 4), 1045–1059. [PubMed doi:10.1093/brain/115.4.1045](#)
- Pruszynski, J.A., King, G.L., Boisse, L., Scott, S.H., Flanagan, J.R., & Munoz, D.P. (2010). Stimulus-locked responses on human arm muscles reveal a rapid neural pathway linking visual input to arm motor output. *The European Journal of Neuroscience*, 32, 1049–1057. [PubMed doi:10.1111/j.1460-9568.2010.07380.x](#)
- Pruszynski, J.A., Kurtzer, I., Nashed, J.Y., Omrani, M., Brouwer, B., & Scott, S.H. (2011). Primary motor cortex underlies multi-joint integration for fast feedback control. *Nature*, 478, 387–390. [PubMed doi:10.1038/nature10436](#)
- Pruszynski, J.A., Kurtzer, I., & Scott, S.H. (2008). Rapid motor responses are appropriately tuned to the metrics of a visuospatial task. *Journal of Neurophysiology*, 100, 224–238. [PubMed doi:10.1152/jn.90262.2008](#)
- Reichenbach, A., Franklin, D.W., Zatka-Haas, P., & Diedrichsen, J. (2014). A dedicated binding mechanism for the visual control of movement. *Current Biology*, 24, 780–785. [PubMed doi:10.1016/j.cub.2014.02.030](#)

- Reynolds, R.F., & Day, B.L. (2012). Direct visuomotor mapping for fast visually-evoked arm movements. *Neuropsychologia*, *50*, 3169–3173. [PubMed doi:10.1016/j.neuropsychologia.2012.10.006](#)
- Saijo, N., Murakami, I., Nishida, S., & Gomi, H. (2005). Large-field visual motion directly induces an involuntary rapid manual following response. *The Journal of Neuroscience*, *25*, 4941–4951. [PubMed doi:10.1523/JNEUROSCI.4143-04.2005](#)
- Saunders, J.A., & Knill, D.C. (2004). Visual feedback control of hand movements. *The Journal of Neuroscience*, *24*, 3223–3234. [PubMed doi:10.1523/JNEUROSCI.4319-03.2004](#)
- Scott, S.H. (2004). Optimal feedback control and the neural basis of volitional motor control. *Nature Reviews. Neuroscience*, *5*, 532–546. [PubMed doi:10.1038/nrn1427](#)
- Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, *7*, 907–915. [PubMed doi:10.1038/nn1309](#)
- Todorov, E., & Jordan, M.I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, *5*, 1226–1235. [PubMed doi:10.1038/nn963](#)
- Voudouris, D., Smeets, J.B.J., & Brenner, E. (2013). Ultra-fast selection of grasping points. *Journal of Neurophysiology*, *110*, 1484–1489. [PubMed doi:10.1152/jn.00066.2013](#)