

PERSPECTIVES

What is adapted in saccadic adaptation?

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The gaze shifts we perform frequently when viewing a scene or reading a text are called saccades. Performing a saccade is a visuomotor process: the visual system localizes a target, for example the next word to be read, and the motor system activates the eye muscles such that the direction of gaze is switched to the target. In-between are the computations from visual target location to eye muscle activation, which are called oculomotor transformations, and which take place in a surprisingly complicated network of cortical and sub-cortical brain areas. Oculomotor transformations are plastic: if a saccade of a particular direction and size consistently fails to reach the intended target the transformation parameters are adjusted. This adjustment, called saccadic adaptation, is experimentally studied by secretly shifting the target while the eye moves, thus creating an apparent error at saccade end which the system corrects by adjusting the saccade parameters. Whether this adaptation occurs at the target localization or at the motor stage is a controversial issue that also touches on the question of what signals the brain uses for perceptual localization.

Changes in subcortical motor structures during saccadic adaptation are documented in many physiological and lesion studies (reviewed in Hopp & Fuchs, 2004). It is thus clear that adaptation at the motor stage exists. Recent studies, however, have found that saccadic adaptation also induces changes to visual localization: visual probes shown before an adapted saccade appear shifted in the direction of adaptation (Bahcall & Kowler, 1999; Awater *et al.* 2005). Pointing to visual targets after saccadic adaptation shows similar mislocalization (Bruno & Morrone, 2007; Cotti *et al.* 2007; Hernandez *et al.* 2008). Congruency of the spatial patterns of mislocalization

and adaptation (the 'adaptation field') shows that saccade targeting and perceptual localization are closely linked (Collins *et al.* 2007).

In an article in this issue of *The Journal of Physiology*, Cotti *et al.* (2009) have used the antisaccade task to differentiate motor control from visual target location, and to study their respective roles in adaptation. In the antisaccade task, whenever a visual target is presented on the right you have to make a saccade to an imaginary copy of the target to the left. Now suppose that normal saccades to the target on the right are adapted. If this adaption involves a change in the representation of the target localization, then the antisaccade to the left should also be adapted because it is directed to a copy of the adapted target. This is indeed what Cotti *et al.* found. (n.b. rightward antisaccades to a visual target on the left also showed adaptation, confirming the well-known involvement of changes in motor structures.)

It gets more complicated, however, since this adaptation of visual targeting was only found for voluntary, not for reactive saccades. Reactive saccades are saccades made in reaction to the sudden appearance of a visual target, for instance a flashing light. Most lab studies use such targets to elicit saccades of a particular direction and size with a predictable reaction time. Voluntary saccades are self-paced, endogenously triggered saccades to internally generated targets, or targets that are constantly visible in a scene. Most saccades we perform in normal circumstances are of this type. Differences between these saccade types are often found in saccadic adaption studies. For instance, after reactive saccades are adapted voluntary saccades to stationary targets at the same location show little adaptation. Thus, different saccade types are controlled and adapted by different pathways. The transfer of voluntary saccade adaptation to antisaccades that was found by Cotti *et al.* is thus clear evidence for a contribution of target localization to adaptation in the voluntary saccade pathway.

Does the lack of antisaccade transfer for the reactive saccades mean that target localization does not contribute to adaptation in the reactive pathway? This issue is more tricky because antisaccades have a peculiar nature: they are instructed

by a visual target but are directed towards an internally generated goal on the opposite side, thus involving a strong voluntary component and an explicit suppression of the reactive saccade to the visual target. Because adaptation of reactive saccades generally transfers poorly to voluntary saccades any transfer to antisaccades might be small. Cotti *et al.* found no significant transfer at the target localization stage but surprisingly strong transfer at the motor stage. Similar results were reported by Collins *et al.* (2008) using a saccade paradigm that shares some similarities with reactive and some with voluntary saccades. Perceptual localization experiments, on the other hand, have shown effects of adaptation on target localization also for reactive saccades (Bahcall & Kowler, 1999; Awater *et al.* 2005; Bruno & Morrone, 2007; Collins *et al.* 2007; Hernandez *et al.* 2008). Further research needs to clarify these differences.

In summary, however, there is now converging evidence that saccadic adaptation is not a single mechanism, and unlikely to act at only a single stage of the oculomotor transformation. Differences between different saccade types and directions of adaptation, influences of saccadic adaption on perceptual localization and pointing responses can best be explained if adaptation takes place at several stages of the oculomotor transformation, including early target localization stages.

References

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