

# Task-relevance is causal in eye movement learning and adaptation

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## Abstract

When a saccadic eye movement does not land accurately on its visual target, subsequent saccades to the same target are subject to a corrective adjustment, which has been called saccade adaptation. Saccade adaptation has emerged as a go-to model for sensorimotor learning. Because observers show limited awareness of image manipulations during

saccades, adaptive changes in saccade amplitude have long been thought to rely on the passive processing of visual error signals. However, it turns out that task-relevance has a modulatory effect on adaptation and that it can even be a sufficient cause for adaptation. Indeed, adaptation can be driven by a shift in task-relevant information even in the absence of a bottom-up visual error. This task-driven adaptation shares similar characteristics to bottom-up adaptation, that is adaptation triggered by a displacement of the eye-movement target. The effect of task-relevance is consistent with an integrated view of the saccadic system, where bottom-up and top-down signals converge to define the saccade target and the orienting of attention. We point to possible neural substrates of top-down adaptation, which largely remains to be elucidated in contrast to the detailed experimental and modeling work linking the cerebellum to bottom-up adaptation.



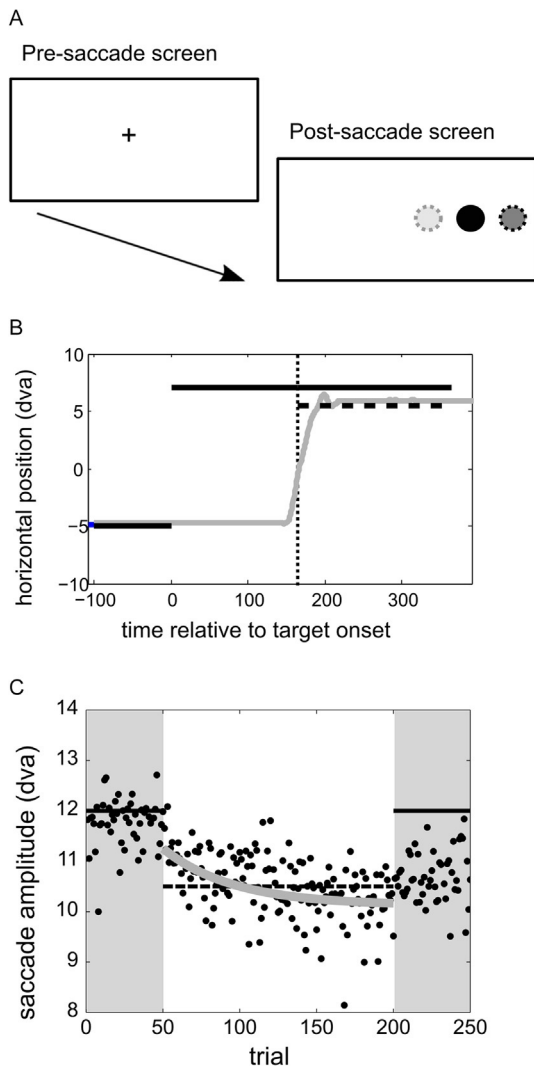
## **1. Introduction to saccade adaptation and the double-step paradigm**

How feedback is used to correct goal-directed actions is a central question in movement neuroscience (for reviews see [Krakauer & Mazzoni, 2011](#); [Shadmehr, Smith, & Krakauer, 2010](#); [Wolpert, Diedrichsen, & Flanagan, 2011](#)). Whether it is for walking in a straight line or riding a bicycle, human brains need to process sensory information, e.g., a combination of visual, vestibular and proprioceptive signals, to be able to reach their intended goal. Learning to do those tasks proficiently can be accomplished by different mechanisms. Explicit knowledge can be used (e.g., when learning to cycle) but implicit responses to sensory feedback are necessary as well (e.g., during walking). Those implicit mechanisms ensure flexible behavior in changing environments. For instance, humans can walk while carrying groceries in the wind without much thought, but the forces applied to balance bags or to walk straight require quick and often automatic adjustment. This error-correction process enables the maintenance of movement accuracy even for the simplest of actions, such as looking at an object of interest or grasping a cup of tea. Knowing how sensorimotor adaptation occurs naturally is essential to understand recovery after injury (e.g., stroke) and to devise effective sensorimotor rehabilitation protocols. Here we will review the evidence for different feedback signals driving saccade adaptation, with a focus on recent studies that attribute top-down control a causal, rather than only modulatory, role in error-correction.

Although sensorimotor learning has been studied extensively with reaching movements adapting to a change in sensory feedback (for reviews

see Krakauer & Mazzoni, 2011; Shadmehr et al., 2010; Wolpert et al., 2011), saccadic eye movements have proven to be a popular testbed to investigate the use of visual feedback in motor control (for a review see Tian, Ethier, Shadmehr, Fujita, & Zee, 2009). There are several advantages to studying those movements. Saccades have a stereotypical velocity profile that is controlled mainly by one parameter, the amplitude of the rotation (Bahill, Clark, & Stark, 1975). Saccades change in response to visual feedback offline, or, put otherwise, there is no online control, which simplifies matters. This means that if a saccade is off target, the central nervous system will need to take note and adjust the motor command for the next time a target at the same location is encountered. Lastly, and most conveniently for the study of implicit adaptation, observers show a limited awareness of manipulations of the visual target location during the execution of a saccade, which has been called *saccadic suppression of image displacement* (Bridgeman, Hendry, & Stark, 1975; for a review see Born, 2019) and may be related to the overall loss of visual sensitivity during saccades, which is called *saccadic suppression of contrast sensitivity* (Dodge, 1900; for reviews see Binda & Morrone, 2018; Ibbotson & Krekelberg, 2011; Wurtz, 2008).

Practically, saccade adaptation has been studied by using variants of the *double-step paradigm* introduced by McLaughlin (1967). In the simplest version, observers are asked to look at a target, which steps to a new location in the periphery. A second step occurs contingent on the execution of the saccade, bringing the target to a slightly different location (Fig. 1A and B). The manipulation requires an eye-tracker providing an online measure of gaze. That way the second target step can be timed to occur during the execution of the saccade, which, as mentioned above, should minimize awareness of the manipulation (e.g., Collins, 2014; Deubel, Wolf, & Hauske, 1986; Souto et al., 2016). Therefore, from the point of view of the observer, a targeting error is injected after the saccade. Because there is no online control, the error can only be corrected on the next trial by adjusting the amplitude of the saccade in response to a similar stimulus. Fig. 1 illustrates the paradigm and the saccade learning that can be elicited. The error-correction is progressive, occurring over tens of trials (Fig. 1C), and it is typically incomplete, reaching a plateau that does not fully correct for the error size being injected. When the manipulation stops (the target remains in place after the first step), saccade amplitude goes back to normal, but gradually, as if adjusting to an error in the opposite direction. Adaptation is also specific to the executed movement amplitude and direction—meaning there is relatively little generalization or transfer of adaptation to



**Fig. 1** The double-step paradigm eliciting bottom-up driven saccade adaptation (McLaughlin, 1967). (A) In this experimental paradigm the observer fixates the center of the screen and is asked to look at a peripheral target when it appears. The target steps forward (in the direction of the saccade, the new position is shown as a dark gray circle) or backward (shown as a light gray circle) contingent on the beginning of the eye movement. (B) Temporal sequence of the double-step. The horizontal position of the target is shown as a black solid line. In a control condition the target stays put after the saccade. In a backward step condition (dashed line) the target steps opposite to the direction of the first step. The eye movement is shown in gray. The step is timed to occur approximately mid-flight during the saccade (vertical dotted line), where eye velocity is at its peak and the step the least noticeable. (C) Sample data, showing how backward steps (dotted line) elicit a gradual reduction of saccade amplitude to match the post-saccade target location over 150 step trials. We can also see a gradual recovery on the post-adaptation trials (solid line). The gray line represents an exponential fit to saccade amplitude during step trials. Adapted from Souto, D., Gegenfurtner, K. R., & Schütz, A. C. (2016). Saccade adaptation and visual uncertainty. *Frontiers in Human Neuroscience*, 10, 227.

new target locations (Noto, Watanabe, & Fuchs, 1999; but see Rolfs, Knapen, & Cavanagh, 2010).

The usefulness of the double-step paradigm in investigating visuomotor learning rests on the assumption that it can mimic the type of adaptation that would occur under natural conditions, for instance if the eye muscles were to suffer an injury. The targeting error could then result from a normal motor command being sent to a weak muscle, ultimately leading to an undershoot. Direct comparison of the two modes of eliciting saccade adaptation indicates that they do indeed share similar mechanisms (Scudder, Batourina, & Tunder, 1998), advocating for the external and ecological validity of the double-step paradigm.

Saccade adaptation, like visuomotor adaptation in general (Leow, Marinovic, de Rugy, & Carroll, 2020), has, until recently, been widely believed to be reflexive. The specificity of transfer in saccade adaptation, the fact there is gradual adaptation back to baseline after the manipulation is removed, and the reduced awareness of the manipulation, combine to suggest that saccade adaptation is a very passive affair, relying on the application of a correction whenever a visual error is found. This idea proved very fruitful for gaining a detailed understanding of how visual feedback is being processed to drive adaptation (for reviews see Herman, Blangero, Madelain, Khan, & Harwood, 2013; Hopp & Fuchs, 2004; Pelisson, Alahyane, Panouilleres, & Tilikete, 2010; Prsa & Thier, 2011). Yet, this view also underestimates the role that task-goals have in shaping adaptation. Even actions that are typically carried out thoughtlessly, such as walking in a straight line, can be subject to top-down control, ensuring further flexibility in changing environments and contexts. For this reason, our goal is to review evidence from investigations that have highlighted the importance of task-relevance in saccade adaptation over the last 10 years.

We will start by reviewing the evidence for bottom-up and top-down control of eye movements in general. We consider as bottom-up any effects that can be attributable to properties and events in the visual input, typically transient and localized changes of the saccade target. Top-down effects are those that arise from a change in the observer's goal or the information they need to process in order to succeed in the task and cannot be attributed to differences in stimulation. We will then proceed by reviewing the evidence establishing a *causal* role for top-down signals in driving saccade adaptation, mainly based on our work showing that a manipulation of task-relevance—

changing the location of the information to process after the saccade, in the absence of a visual transient—is a sufficient (if not necessary) driver.<sup>a</sup>



## 2. Bottom-up and top-down control of saccades

When thinking about the role of top-down and bottom-up control of eye movements, it is important to keep in mind why humans and non-human primates need to shift their gaze in the first place. Contrary to our perceptual experience, visual processing is not homogeneous across the visual field. Contrast sensitivity and acuity peak at the center of the visual field, the fovea, and decline toward the periphery. Furthermore, peripheral object recognition is more impaired by neighboring objects, which is called crowding (for reviews see [Rosenholtz, 2016](#); [Simpson, 2017](#); [Strasburger, 2020](#); [Strasburger, Rentschler, & Juttner, 2011](#); [Whitney & Levi, 2011](#); [Yu, Chaplin, & Rosa, 2015](#)). To benefit from foveal vision at different places in the visual field, primates can shift their gaze by saccadic eye movements up to about three or four times per second.

There is a large body of literature on how eye movements are controlled by different bottom-up and top-down signals (for reviews see [Hayhoe, 2017](#); [Schütz, Braun, & Gegenfurtner, 2011](#)). As examples of bottom-up control, visually salient regions (e.g., [Itti & Koch, 2001](#)) and objects attract more fixations ([Einhäuser, Spain, & Perona, 2008](#)). Examples of top-down control are given by expected reward ([Milstein & Dorris, 2007](#); but see [Wolf, Heuer, Schubö, & Schütz, 2017](#)) and behavioral-task goals (e.g., making a sandwich) in predicting fixations—e.g., one fixates the knife before using it to spread the jam—([Hayhoe, 2000](#); [Land, Mennie, & Rusted, 1999](#)). It goes without saying that because only one eye movement is possible at any point in time, these different signals need to be traded-off. Several studies have shown that eye movements tell us something about how this trade-off is resolved (e.g., [Markowitz, Shewcraft, Wong, & Pesaran, 2011](#); [Schütz, Lossin, & Gegenfurtner, 2015](#); [Schütz, Trommershäuser, & Gegenfurtner, 2012](#)). For instance, when a highly salient region and a high-value region yielding a reward compete for

<sup>a</sup> Aside from eliciting motor adaptation, the double-step manipulation also induces a corresponding change in the perception of the target location in the periphery, which could suggest a remapping of space for perception and action rather than specifically oculomotor mechanism (e.g., [Awater, Burr, Lappe, Morrone, & Goldberg, 2005](#); [Bahcall & Kowler, 1999](#); [Collins & Dore-Mazars, 2006](#); [Zimmermann & Lappe, 2010](#)). For the sake of clarity, we will review exclusively oculomotor error-correction.

saccades, the endpoint depends on the latency of the saccade and the available time to resolve the competition: short-latency saccades land closer to the salient region while long-latency ones land closer to the high-value region (Schütz et al., 2012).

Different types of saccades have been found to be preferentially controlled by different neural substrates (McDowell, Dyckman, Austin, & Clementz, 2008; Mort et al., 2003). Accordingly, there can be little transfer of adaption from one saccade type to another. Three major types are typically distinguished. *Reactive* saccades are triggered by the sudden appearance of a stimulus in the periphery and are characterized by relatively short saccade latencies. *Delayed* and *scanning* saccades are executed to stable visual references and are therefore supposed to be under top-down control or voluntary. This is also true of *memory-guided* saccades, executed toward the memorized location of stimuli that have disappeared before and characterized by longer latencies and lower accuracy. Reactive saccades, and sometimes also voluntary ones, are usually tested with the double-step paradigm. There is a limited transfer of adaptation between reactive and voluntary saccades (e.g., Gancarz & Grossberg, 1999; Hopp & Fuchs, 2010; Kojima, Fuchs, & Soetedjo, 2015), suggesting that those saccade types involve partially different neural substrates either in their execution or error-correction mechanisms.



### 3. Bottom-up error signals for saccade adaptation

Previous review papers have described in great detail the type of error signals driving saccade adaptation (Herman et al., 2013; Hopp & Fuchs, 2004; Pelisson et al., 2010). We will only provide a brief outline of those signals, which we will later contrast with the effect of task-relevance.

#### 3.1 Retinal error

Since the goal of saccades is to bring an object of interest toward the fovea, an obvious candidate error signal in driving saccade adaptation is the retinal error observed after the saccade; as defined by the distance between the fovea and the target in retinal coordinates. In this case, target undershoots would generate a compensatory lengthening of subsequent saccades and overshoots a shortening. One problem with this simple account is that saccades normally undershoot the target and adaptation preserves this undershoot when the target is stepped backward (Schütz, Kerzel, & Souto, 2014; Wong & Shelhamer, 2011). Accounting for this finding would require an asymmetric weighting of retinal errors, with higher tolerance for undershoots and less

tolerance for overshoots. Several reasons for the preference for undershoots have been proposed, including the minimization of flight time (Harris, 1995; Harris & Wolpert, 1998), faster correction of undershoots by secondary saccades (Lisi, Solomon, & Morgan, 2019; Ohl, Brandt, & Kliegl, 2011, 2013) and nonlinearities in the neural representation of space in the superior colliculus (Vitu, Casteau, Adeli, Zelinsky, & Castet, 2017). However, as we will discuss next, the tendency for saccades to undershoot their target may be irrelevant to saccade adaptation<sup>b</sup> given the clear evidence that retinal errors are not the primary signals driving saccade adaptation.

### 3.2 Prediction error

Several studies have shown that the signal driving saccade adaptation is not retinal error but prediction error, defined as the discrepancy between the predicted and actual retinal location of the target after the saccade. Unlike retinal error, prediction error is not directly accessible. The latter needs to be computed from two different signals: an estimate of the target eccentricity before the saccade and information about the saccade metrics are both needed to predict the retinal location where the target will fall after the saccade. Theoretically, the information about the saccade metrics could come either from an efference copy (von Holst & Mittelstaedt, 1950), also called corollary discharge (Sperry, 1950) that is sent from motor regions to sensory areas before the saccade (for a review see Sommer & Wurtz, 2008), or, alternatively, from proprioceptive signals coming from the eye muscles during or after the saccade (Wang, Zhang, Cohen, & Goldberg, 2007; Steinbach, 1987). In practice, the efference copy signal must dominate, because saccade adaptation is intact after sectioning the nerve that carries proprioceptive information coming from eye muscles (Lewis, Zee, Hayman, & Tamargo, 2001).

How can retinal and prediction errors be disentangled? In the double-step paradigm, shifting the target during the saccade will add a systematic prediction error. The retinal error will change because of the manipulation as well. Nonetheless, retinal and prediction errors can be decorrelated. For instance, the backward step can be the size of the natural saccade undershoot, meaning that the retinal error becomes zero, but the prediction error exists since the target stepped.

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<sup>b</sup> Which is not to say that increasing saccade amplitude and decreasing it imply the same mechanisms (Ethier, Zee, & Shadmehr, 2008a; Golla et al., 2008).



In one manipulation, the target is stepped backward during the saccade, but to such a small extent that the saccade still undershoots the target (Wong & Shelhamer, 2011). The retinal error should lead to an increase in saccade amplitude, whereas the prediction error signal has an opposite sign, and should lead to a decrease in saccade amplitude. In this situation, saccade adaptation follows the direction of the prediction error. In another ingenious manipulation, Collins and Wallman (2012) could show how the predictive signal is a much stronger drive compared to the retinal error. In one condition the target is extinguished during the saccade, but only for saccades that are smaller or larger (depending on the session) than the median saccade amplitude over the last 50 trials (Collins & Wallman, 2012). For instance, in one condition, the observer does not receive any postsaccadic feedback for saccades larger than the median saccade amplitude. In this condition a small reduction of saccade amplitudes occurs, although the target is not displaced during the saccade. Therefore, saccade adaptation can be explained by the imbalance of error signals (whether retinal or predictive) indicating overshoots and those indicating undershoots. The critical finding concerns a second session, in which the same retinal errors are replayed, that is the target is displayed at the end of the saccade at the same retinal location where it fell on the previous session on that particular trial. The replay condition reproduces the same imbalance of retinal error signals experienced in the first session. However, in the replay condition, there is no efference copy signal accounting for the retinal errors, meaning that there is a stronger prediction error in that session. Although retinal errors are identical in both conditions, adaptation is much more pronounced in the replay condition, establishing the dominance of the prediction error in driving saccade adaptation. More generally, the dominance of prediction errors fits an internal model account of sensorimotor adaptation (e.g., in reaching or adaptation to force fields) where a feedforward model is built, using an efference copy, to predict the sensory outcomes of any movement to compare against incoming information. Mismatch errors thus computed can have multiple uses, not only in online and offline movement control, but also in assigning credit (which muscle is responsible for the error) or agency (was it an internal or external cause?) (for a review see Wolpert et al., 2011).

### 3.3 Motor correction

Another error signal that could be used to drive adaptation comes from motor correction. At the beginning of adaptation, the initial saccade, also

called primary saccade, is typically followed by a secondary (or corrective) saccade that reduces the error of the primary saccade. The goal of adaptation could be to minimize those corrections depending on their direction. However, studies showed that there is little correlation between corrective saccades and adaptation of the primary saccade. Adaptation is still present, even if corrective saccades are eliminated, either by shifting the target only briefly after the saccade (Wallman & Fuchs, 1998) or by using large saccade targets that do not trigger corrections (Bahcall & Kowler, 2000). Therefore, adaptation does not require a motor correction to occur.

In fact, one may argue the other way around that the ability to correct errors of the primary saccade reduces the necessity to adapt the primary saccade. Indeed, adaptation is strongly reduced if the target is extinguished at saccade onset and only reappears with a certain delay (Bahcall & Kowler, 2000; Fujita, Amagai, Minakawa, & Aoki, 2002; Minkawa, Fujita, & Amagai, 1997; Shafer, Noto, & Fuchs, 2000). Under these circumstances, the oculomotor system chooses to correct those temporally delayed errors by a corrective saccade during the delay period instead of adapting the primary saccade.

### 3.4 Exogenous visual attention

Although prediction errors are believed to be the main driver of saccade adaptation, several studies indicate that visual selective attention, the mechanism used to prioritize visual information, can by itself generate adaptation (Herman et al., 2013). Those studies concern specifically exogenous orienting of attention. Exogenous orienting refers to the reflexive allocation of visual attention allowed by the presentation of a transient stimulus, e.g., a peripherally flashed dot. In the double-step paradigm, the intra-saccadic step can itself be understood as a transient stimulus. However, its impact in capturing attention, as do transients during fixation, is attenuated by saccadic suppression of displacement and saccadic suppression of contrast sensitivity. In Khan, McFadden, Harwood, and Wallman's (2014) paradigm, upon detection of a saccade toward a peripheral target, a distractor is displayed for a brief time along with the target (a black dot), which is displayed for longer. Importantly, the target to fixate remains the same throughout trials, and is easy to visually distinguish from the distractors, which were chosen to maximize their salience and novelty (e.g., animals and anime characters). Distractors are meant to generate an *attentional error* signal that would be corrected depending on whether distractors were located forward or

backward of the target ( $+/- 3^\circ$ , meaning degrees of visual angle). Those salient distractors can generate a modest amount of adaptation as indicated by the difference between saccade amplitudes with forward and backward distractors. This effect appears to build up across trials, instead of showing more adaptation at the beginning, a feature that departs from the classical observation of adaptation following an exponential curve (Fig. 1C). Adaptation is also maintained after the distractors are removed. The effect of the distractors depends on their salience, as adaptation is measurably smaller with random dots instead of meaningful images. The influence of salience, and possibly novelty, could explain why another study found no effect of distractors on adaptation (Madelain, Harwood, Herman, & Wallman, 2010).

The effect of exogenous attention on adaptation can be understood within the context of the interconnectedness between visual orienting and eye movement programming structures at the subcortical and cortical level. For instance, visual transients interfere with eye movement signals in the superior colliculus (Mays & Sparks, 1980; White & Munoz, 2012). More generally, there is a well-known *bi*-directional link between the allocation of attention and the execution of eye movements. This link has been summed up in the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987), postulating that attention shifts entail a motor plan for an eye movement to the attentional target, whether it is ultimately executed or not. Conversely, saccades entail a mandatory shift of attention to the saccade target (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995). Not all the predictions of the premotor theory of attention have been borne out (for a review see Smith & Schenk, 2012), especially regarding the idea that all visual orienting entails a saccade program. However, this tenet may especially be true for exogenous attention in relation to reactive saccades (Smith, Schenk, & Rorden, 2012). We may then explain the effect of distractors on saccade adaptation by assuming that the visual signals driving saccades are also those driving attentional selection.

In the context of saccade adaptation, the *bi*-directional link postulated by the premotor theory is most tellingly demonstrated by the finding that one is able to adapt exogenous shifts of attention and that this leads to saccade adaptation (McFadden, Khan, & Wallman, 2002). In that paradigm, a peripheral cue induces a shift of attention, while subjects have to maintain central fixation. After an interval, which corresponds to the average time it takes to shift attention, the cue is stepped by  $3^\circ$  either closer or further away from

fixation. This induces adaptation of attention shifts that shares many properties with saccade adaptation. Most importantly, subsequently tested saccades are adapted according to the step direction of the attentional cue although no saccades are executed during the adaptation procedure. In the reverse direction, recent studies have indicated that saccade adaptation can amplify the effect of exogenous (Habchi et al., 2015) and endogenous (Nicolas, Bidet-Caulet, & Pélisson, 2019) shifts of attention, even though the attentional task does not require a saccade. Although the specific mechanism by which this transfer is observed remains to be resolved, it speaks for the interrelation between target selection mechanisms guiding perceptual and oculomotor selection.

To sum up, exogenous attention generates an error signal that can drive saccade adaptation. We find interesting that others have proposed that exogenous attention is itself driven by a prediction error, with attention being grabbed by unexpected events (van Boxtel & Lu, 2013). In that predictive coding framework the visual system favors the processing of mismatch errors, by shifting attention to unlikely changes in the visual field, in an attempt to minimize uncertainty (see also Smout, Tang, Garrido, & Mattingley, 2019). In concrete terms, what are the chances that an object will move during a saccade? It is much more likely to have continuity, that is for objects to maintain their position across saccades. When continuity is broken, it is a noteworthy event that needs processing and correcting if systematic. This view, linking prediction and attentional signals, fits nicely with the dominance of prediction errors in driving adaptation.

### 3.5 Contextual control of adaptation

The eye movement system does not simply generalize what is learned from one error to all eye movements. Instead, learning can be specific for a given context, allowing the system to switch between different adaptation states depending on the presence of simple cues. Effective cues are eye position before the saccade (Alahyane & Pélisson, 2004; Shelhamer & Clendaniel, 2002; Tian & Zee, 2010) and the target's movement before the saccade (Azadi & Harwood, 2014). Other target features, such as color, shape or temporal flicker have led to inconsistent results (Azadi & Harwood, 2014; Deubel, 2005; Herman, Harwood, & Wallman, 2009) and a coherent picture of which features can be used as cues for discriminative learning is still missing. Nevertheless, the evidence for contextual control suggests that saccade adaptation is more than a simple error-correction mechanism, whether it is a top-down or bottom-up higher-level signal that establishes the adaptation context.



## 4. Modulation of bottom-up driven adaptation by top-down signals

So far, we have considered the role of passive processing of diverse error signals in determining saccade adaptation. Recent studies have also sought to investigate the influence of top-down signals, mainly as a modulatory factor. One way has been to manipulate the availability of attentional resources available to process error signals (Gerardin, Nicolas, Farnè, & Pélisson, 2015). Another way has been to manipulate the intrinsic or explicit value of the target stimulus (Meermeier, Gremmler, & Lappe, 2016), thereby enhancing the relevance of adapting eye movements. We must note here that while we discuss the effects of attention, reward and information separately, in keeping with a long research tradition, the definition of those concepts does not always allow clear separation, in addition to being difficult to distinguish empirically (for reviews see Gottlieb, Balan, Oristaglio, & Schneider, 2009; Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014; Maunsell, 2004; for an example see Marx & Einhäuser, 2015).

### 4.1 Endogenous visual attention

As explained above (Section 3.4) visual attention and eye movements share common control mechanisms, so one can expect that voluntarily (endogenously) selecting stimuli that are not the target of the saccade will affect the ability to process the error signal driving adaptation. Modulating visual attention available for the target, either by drawing attention to the target or diverting it away from it, can have diverse consequences. Visual attention has the effect of improving detection and perceptual discrimination (for a review see Carrasco, 2011). It could follow that an enhanced error signal may generate more adaptation. However, since the rate of saccade adaptation varies little when comparing 10% and 100% contrast targets (Souto et al., 2016), enhancing the error signal by paying more attention to the target is not likely to lead to stronger saccade adaptation. Things are different when there is a competition between signals (Desimone, 1998; Desimone & Duncan, 1995). In that case, when the effect of attention is to select one signal and suppress the other, large effects can be observed either on neural representations or behavior. All-or-none responses (winner-takes-all) can be observed depending on which object is the designated target. Madelain et al. showed evidence for this type of selectivity in two studies. Humans are able to adapt their saccades just as well in the presence of a distractor that steps in the same way as the saccade target but in a different direction, even

though in physical terms it provides an equally salient error signal as the target (Madelain et al., 2010). Similarly, adaptation can be specific to the position changes of the eye movement target, while ignoring a shift of the background (Madelain, Herman, & Harwood, 2013). Hence, humans can voluntarily choose which target to adapt to. A recent study demonstrates this further by showing that observers can reduce the amount of adaptation by being asked to avoid an adjustment of saccade amplitude by looking at the location of the target after the first step and not at its location after the second step (Heins, Meermeier, & Lappe, 2019). Volition could eliminate forward adaptation, while backward adaptation was only reduced in magnitude.

One study manipulated endogenous attention by adding an easy or hard perceptual discrimination task to the double-step paradigm (Gerardin et al., 2015). The saccade target is a plaid that turns into an oriented grating presented briefly (masked) after the saccade. Importantly, there is a difficult discrimination condition and an easy discrimination condition for every target, as gratings have a slight tilt relative to the horizontal or vertical (difficult task), but clearly align with either axis (easy task). Presumably, the hard discrimination should engage more attentional resources, which should result in a better adaptation in that condition. Indeed, both with reactive and voluntary saccades, adaptation of saccade amplitudes is more complete with the difficult discrimination, demonstrating the important role of endogenous attention. As explained above, the effects of visual attention are in general much less dramatic when there is no competition between objects to select from. The relatively robust effects found by Gerardin et al. (2015) could suggest that the amount of visual attention allocated to the target has an impact on binding error signals to movement representations (Reichenbach, Franklin, Zatzka-Haas, & Diedrichsen, 2014), rather than the mere effect of error signal enhancement. The work of Ditterich, Eggert, and Straube (2000) suggests also the importance of the size of the attentional window (the size of the relevant target area) in determining the visual error that is adapted. They found that intra-saccadic background shifts impact adaptation to a target jump only when the target is large and the bottom-up error is contained within the attentional window.

## 4.2 Stimulus properties: Informational value and reward

So far, we described paradigms in which the target is most often a tiny dot on a gray or black screen, a grating at most. Those stimuli are not only a far cry from natural stimulation, but they are also very uninformative, given that

saccades to the same targets are repeated up to hundreds of trials. In natural situations, humans mostly look at objects because they want to seek specific information about their environment and use that information in the context of a task (e.g., determine safe foot placement during walking, find a friend at a party). We can call the relative visibility of a target in the periphery before a saccade and in the fovea after the saccade the information gain of the saccade (i.e., it is much easier to recognize a face when looking at it). The informational value of a target then depends on its relevance for mastering the current task. An ideal observer that maximizes information gain for every fixation can be a good fit to human visual search patterns in some conditions (Najemnik & Geisler, 2005, 2008; Peterson & Eckstein, 2012), while human searchers are clearly not ideal in other conditions (Eckstein, Schoonveld, Zhang, Mack, & Akbas, 2015; Morvan & Maloney, 2012; Nowakowska, Clarke, Sahraie, & Hunt, 2016; Vergheze, 2012). The value of information gain is often relative to the current task-goals; e.g., if walking on cobbled stones, fixations to the ground hold more value in avoiding slippage (Matthis, Yates, & Hayhoe, 2018; 't Hart et al., 2009), but some stimuli are intrinsically more relevant to our survival than others, such as faces. Therefore, natural stimuli differ in their informational value and relevance for the goals of the organism.

Reflecting the overall importance of the target's informational value, saccade adaptation is more complete when photos of attractive women (participants being women for the most part too) are used as saccade targets compared to noise patches matched for luminance and spatial frequency content (Meermeier et al., 2016). No clear difference was found on learning rate. The finding can be interpreted in at least two ways. One is that biological stimuli are deemed more relevant to survival and are therefore inherently rewarding, regardless of the task. A second is that those stimuli have higher novelty compared to noise. Even though the noise pattern was different on every trial it can be assigned the same meaning. A follow-up study showed that the novelty of the stimulus indeed plays a role, since saccade adaptation is more complete when photos of different woman are shown on every trial compared to when the same image is repeated (Meermeier, Gremmler, & Lappe, 2017).

Previewing the discussion of explicit rewards in the next section, we can note that the effect of informational value on saccade adaptation is mediated by biological and varied stimuli providing a higher implicit reward than artificial and repetitive stimuli—put otherwise there is more to gain from seeing the target. However, the facilitation of adaptation seems to be specific to

primary reinforcers (such as meaningful images vs. noise, or novel vs. familiar images) but not to secondary reinforcers (such as words vs. nonwords or high vs. low reward video game images) (Meermeier, Gremmler, Richert, Eckermann, & Lappe, 2017), which may suggest that the benefit of biological content and novelty has been built over a long period of time (perhaps a lifetime) and cannot be mimicked by arbitrarily assigning value in the shorter term. However, the advantage of primary reinforcers might be restricted to a situation in which there is no requirement to process the target information. As we will see below, others have shown rapid effects of abstract reward when reward is the only signal driving adaptation (Madelain, Paeye, & Wallman, 2011).

In addition, motor accuracy itself could be considered a reinforcer. This could be because accuracy is a desirable property of the motor system or because it is costly (e.g., metabolically) to generate corrective saccades, although we have seen above that saccade adaptation is similar in the absence of corrective saccades.

Finally, the effect of informational value on saccade adaptation could as well be mediated by visual attention, with attention being paid to more relevant and novel stimuli (e.g., Failing & Theeuwes, 2018).



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## 5. Top-down signals driving adaptation

We have seen so far how top-down signals can exert modulatory control over saccade adaptation. In that case, adaptation was triggered by bottom-up errors (an intra-saccadic target step). Top-down signals may increase the priority of the target depending on its informational value and biological relevance. In this section, we focus on the potential for top-down signals to causally drive saccade adaptation by themselves, in the absence of a bottom-up sensory error, whether it is a retinal error or a prediction error.

### 5.1 Reward as a sufficient signal

Reward plays an important role for the control of eye movements in general (Gottlieb et al., 2014; Madelain, Paeye, & Darcheville, 2011) and the expectation of reward affects eye movements in multiple ways: for instance, it can reduce saccade latencies to targets (Milstein & Dorris, 2007; but see Wolf et al., 2017), determine target selection and modulate the effect of distractors in visual search (Hickey & van Zoest, 2012; Theeuwes & Belopolsky, 2012). As we have discussed above (Section 4.2), explicit reward does not always



result in enhanced saccade adaptation (Meermeier, Gremmler, Richert, et al., 2017). However, monkeys show faster saccade adaptation on a side that is rewarded by applesauce compared to the opposite, unrewarded side (Kojima & Soetedjo, 2017). As noted above, the effect of rewards may take time to build up, but critically it may depend on the use of primary reinforcers such as food.

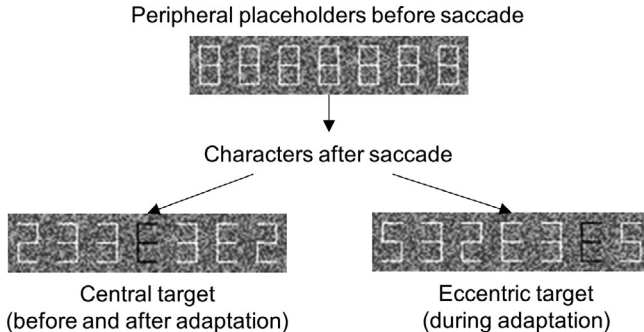
Beyond the modulatory effects of reward on saccade adaptation, there is also evidence for reward being a sufficient signal in driving saccade adaptation. In a single-step saccade task, Madelain, Paeye, and Wallman (2011) rewarded saccades shorter or longer than a running average while nulling retinal errors after the saccade by bringing the target to the measured gaze location. Rewarding shorter saccades leads to a gradual decrease in amplitudes, and a gradual increase when rewarding larger saccades. This effect demonstrates the sufficient nature of the reward since there is no retinal error and the distribution of prediction errors should be unbiased. One may ask whether those saccades show the signature of implicit adaptation, in contrast to adaptation due to strategic (voluntary) behavior aimed at maximizing reward. When adaptation is implicit, we expect some *inertia*: amplitudes adapt gradually and when the driving signal is removed, they come back to normal gradually too. Explicit adaptation, on the other hand, is expected to recover as soon as the observer realizes that the reward has stopped or that there is no postsaccadic error. In favor of implicit adaptation, the saccade amplitude change persists after the reward manipulation for several trials. One may ask further whether reward adaptation is quantitatively similar to the bottom-up driven adaptation in the double-step paradigm. In fact, reward-driven adaptation is quite similar in many aspects, such as the magnitude of the effect, generalization or transfer to other amplitudes and starting positions, and the rate of recovery (Madelain, Paeye, & Wallman, 2011). Based on those similarities, the authors went a step further to propose that the maximization of reward is the driving force in classical adaptation too (i.e., in the double-step paradigm), where, as noted above, informational gain provides an implicit reward. The finding that the content of the post-saccadic image modulates adaptation only if its postsaccadic processing time is limited (Meermeier et al., 2016) supports this notion. However, we may argue that robust adaptation is obtained even with the type of uninformative targets typically used in a double-step paradigm: they are supra-threshold arbitrary shapes, repeated for hundreds of trials. Therefore, explicit reward might be thought of as a supplementary signal, which along with bottom-up visual errors is able to generate saccade adaptation.

## 5.2 Task-relevance: Target selection as a sufficient signal

As mentioned in Section 2, eye movements are strongly driven by task demands (for reviews see Gottlieb, 2012; Hayhoe, 2017; Schütz et al., 2011). When stimulation is predictable, they are directed to regions in space and time that are informative in relation to the task at hand, such as looking ahead of the point of contact of a bouncing cricket ball when the task is to bat the ball (Land, 2006; Land & McLeod, 2000). If the task is to find your car keys, your eye movements will be directed to peripheral smudges of the right size and color (for reviews see Eckstein, 2011; Wolfe, 2010). We argue that when a saccade falls short of the location where information needs to be processed, this *selection error* is in itself a sufficient driving signal for saccade adaptation.

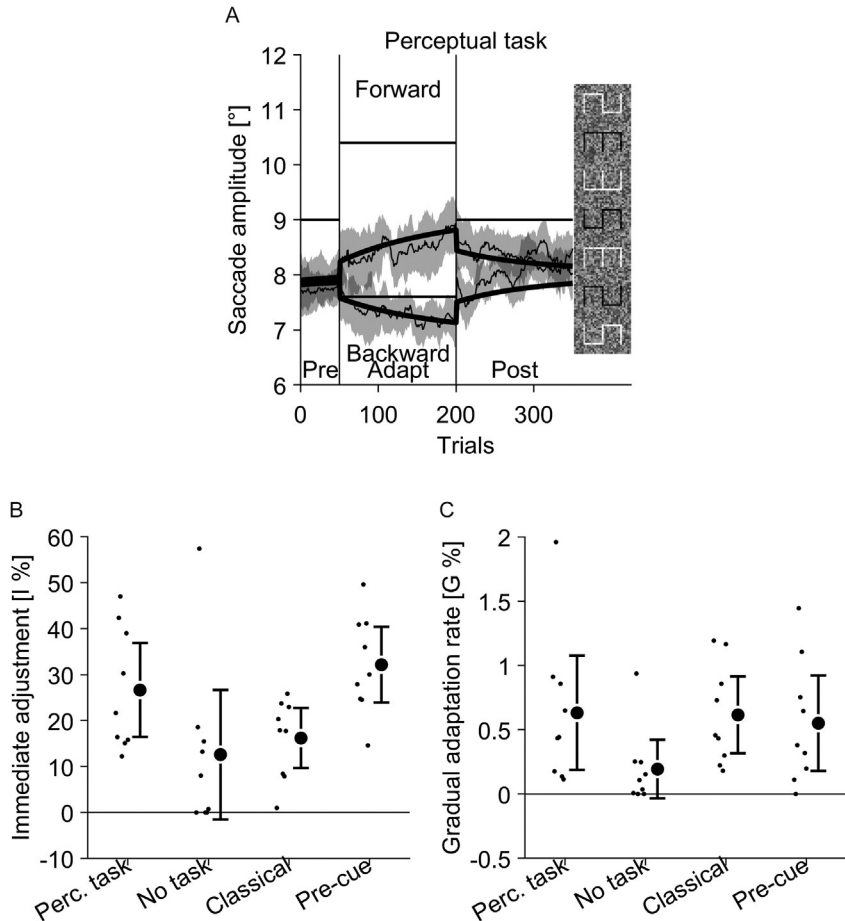
To investigate the role of task-relevance on saccade adaptation in the lab, our strategy has been to devise a task that dissociates the information that the observer needs to process after the saccade from the bottom-up error signal (Schütz et al., 2014; Schütz & Souto, 2015; Wolf, Wagner, & Schütz, 2019).

Fig. 2 shows the stimuli in the first series of experiments (Schütz et al., 2014). The observer has to saccade to an array of placeholders. Their second



**Fig. 2** Stimuli and experimental paradigm to study how task-relevance can drive saccade adaptation in Schütz et al. (2014). Before the saccade, an array of placeholders embedded in a noise background were shown in the periphery. Upon saccade onset, the placeholders were replaced by one target (black) and several distractors (white). In baseline trials before and after adaptation, the target was always shown in the center of the array. In adaptation trials, the target was always shown at the same eccentric location in the array. Since leftward and rightward saccades were interleaved, the eccentric target was either closer to the initial fixation position (eliciting backward adaptation) or further away (eliciting forward adaptation). Note also that the saccade target became the location of the next fixation point and the saccade target direction was randomly selected. Adapted from Schütz, A. C., Kerzel, D., & Souto, D. (2014). Saccadic adaptation induced by a perceptual task. *Journal of Vision*, 14(5), 4, 1–19.

task is to categorize the identity of the letter appearing at a specific location in the array after the saccade. The designated letter is black, while the others are white. We could contrast several conditions to single out the effect of task-relevance on the adaptation of saccade amplitude, as summarized in Fig. 3A. First, even though there is no intra-saccadic step, and the contrast



**Fig. 3** Results of the on-axis adaptation from Schütz et al. (2014). (A) Shows horizontal saccade amplitude when the observer performed the perceptual task (cf. Fig. 2). (B) Magnitude of immediate adaptation. (C) Magnitude of gradual adaptation. (B and C) Small dots represent individual participants; large dots the mean across participants. Error bars represent 95% confidence intervals. The classical condition refers to applying the double-step paradigm to the array. Redrawn from Schütz, A. C., Kerzel, D., & Souto, D. (2014). Saccadic adaptation induced by a perceptual task. *Journal of Vision*, 14(5), 4, 1–19.

of the target letter is no different from the non-target letters, we find a gradual increase in saccade amplitudes when the relevant information is ahead of the array-center and a gradual reduction of amplitudes when it is backward from the array-center. On a later phase, when the target letter reverts to the center there is a gradual recovery to the initial saccade amplitude. This effect is likely to be driven by task-relevance, since the location of the array does not change during the saccade, generating no retinal error or prediction error.

An important feature of the data analysis is that we tried to disentangle quick and gradual changes in amplitude by fitting a two hidden-state model. The quick or immediate adaptation is likely to represent an explicit, strategic effect, which could correspond to the knowledge that participants need to aim for an eccentric location in the array. The slow component is likely to correspond to what we observe in bottom-up driven adaptation in the double-step paradigm, a gradual and presumably implicit adjustment that needs to be reverted back once manipulation ends. Our fits indicate the presence of both components (Fig. 3B and C). Given, that an explicit component exists, why don't observers aim directly at the target? When looking at an object or a group of objects, saccades are subject to the global effect (Findlay, 1982; Van der Stigchel & Nijboer, 2011), a tendency to land on the center-of-gravity of a configuration or group of objects. The global effect, as well as the limited resolution of peripheral vision (i.e., crowding) may combine to limit the ability to aim straight to the black letter.

We may think that the effect of task-relevance, instead of representing a pure top-down signal, is actually reflecting the exogenous effect of attention that we have reviewed earlier in Section 3.4. Indeed, although the contrast of the black letter is the same as the others, it is a singleton (a feature that pops out from its background), which are known to be able to capture visual attention (e.g., Theeuwes, de Vries, & Godijn, 2003). Further, as we have discussed earlier, salient distractors can drive saccade adaptation (Khan et al., 2014). Nonetheless, we can confidently rule out this hypothesis by contrasting the effect of performing the dual task (perceptual categorization + saccade) to the effect of performing only a saccade task, meaning the observers need only to look at the peripheral array and ignore the black letter. In the saccade task, there is virtually no saccade adaptation, indicating that the effect of task-relevance is unspoiled by exogenous cueing.

We sought also to compare the saccade adaptation driven by task-relevance to saccade adaptation elicited by the prediction error in the double-step paradigm. To do so, we mimicked the double-step paradigm

by moving the entire array backward or forward when the saccade is detected, while the black, task-relevant letter remains in the center of the array throughout the experiment. The results, shown in Fig. 3B and C, indicate that both the immediate and gradual adjustment are remarkably similar across paradigms, even though one is driven by a top-down error signal and the other one by a bottom-up error signal.

Although similarities with saccade adaptation in the double-step paradigm suggest otherwise, we can still wonder whether the effect of task-relevance is due to a genuine reconfiguration of visuomotor mapping. More concretely, observers, being aware of the perceptual task target, could be consciously targeting something different than the center of the array. We argued that we also observe a gradual adaptation and recovery. But it could be argued that observers might be slow to pick up on this information after dozens of trials of doing something else. Fig. 3B and C shows the results of an experiment designed to address those concerns, by presenting the target letter all along (before and after the saccade, called pre-cued condition) and thereby effectively removing all ambiguity as to where it would be located after the saccade. We observed the same effects, including the long recovery, which indicates that it is unlikely that the effect of task-relevance is purely an explicit, strategic process. We can also note that the same point can be made of the double-step paradigm. Part of the learning observed can be explicit too (as defined by the presence of a fast adapting process), at least with reactive saccades (van Es & Knapen, 2019). In fact, the contribution of an explicit component might explain faster adaptation in humans than in monkeys in the double-step paradigm (Straube, Fuchs, Usher, & Robinson, 1997).

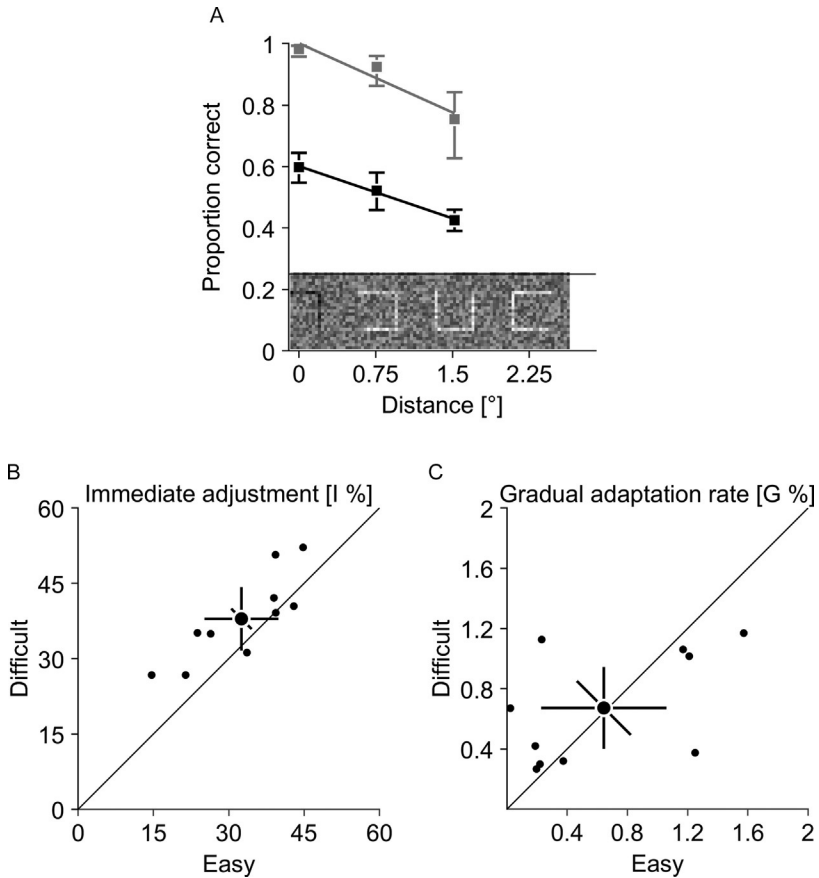
We further asked about what causes the effect of the task-relevance. One possibility, as put forth by others, is that information gain acts as a reinforcer (Madelain, Paeye, & Wallman, 2011). In our paradigm, looking at the target letter increases the number of correct responses, and this informational gain could provide an implicit reward driving adaptation. Secondly, there is also a corresponding reduction in the amount of negative feedback after perceptual errors (a beep) (Schütz et al., 2014). This could lead to reinforcing saccades landing on the target letter. A third possibility is that target selection acts as a substitute for the visual (prediction) error. More precisely, saccades might not be evaluated according to the difference between the *predicted* and the actual landing position, but between the location with the highest informational value (as determined by the task here) and the actual landing position.

A second study allowed us to narrow down on possible interpretations (Schütz & Souto, 2015). In that study, we tested off-axis adaptation, meaning that the task-relevant information was shifted vertically, leading to adaptation of saccade direction rather than amplitude (Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008; Schütz & Souto, 2011; Wallman & Fuchs, 1998). We found that this paradigm maximized adaptation in the earlier study and therefore used it in our second study again. To generate off-axis adaptation the perceptual target is placed either upwards or downwards from the center, orthogonal to the direction of the saccade. First, we replicated the finding that a more difficult task (a narrower gap in a Landolt “C”) generates faster adaptation (Fig. 4) (Gerardin et al., 2015). Our fits of the two-stage model indicated that the boost in adaptation with the more difficult task is only observed on the immediate (Fig. 4B) but not in the gradual adjustment (Fig. 4C). Perhaps increasing the difficulty of the discrimination increases attention to the target and the likelihood of consciously aiming to the target location rather than the whole array. Second, we manipulated the feedback, to be able to rule out its influence on adaptation. We showed that random (unrelated to performance) and valid feedback (a beep indicates incorrect responses) elicit a very similar amount of adaptation. If anything, the random feedback appears to have speeded up the gradual adjustments, but not the immediate adjustments.

Those findings point out that target selection is sufficient to explain the effect of saccade adaptation driven by task-relevance. Informational gain, as manipulated by task-difficulty, did not affect gradual adaptation, nor did the administration of random feedback, suggesting that the primary signal driving adaptation results from attentional mechanisms responsible for saccade target selection.

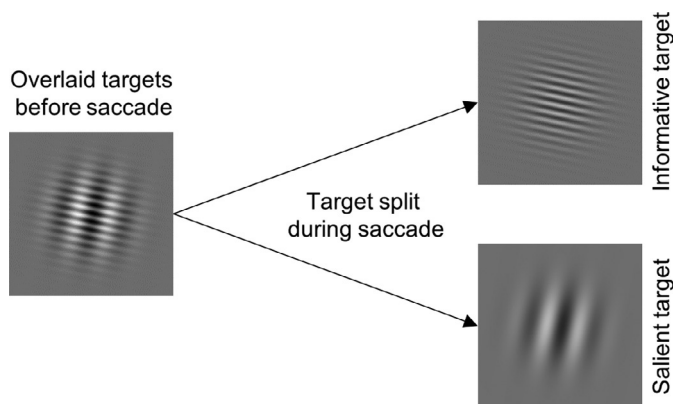
### 5.3 Task-relevance: Priority among competing targets

Our first two studies showed that task-relevance can trigger saccade adaptation even in the absence of a bottom-up visual error. However, adaptation (the gradual change) was not clearly modulated by the information gain related to the perceptual task. Wolf et al. (2019) tested whether informational gain plays a role in adaptation when there is a competition between two task-relevant locations. We noted earlier how the effects of target selection on behavior are larger when there is more than one object to select from. Informational gain would then be more likely to determine target selection and drive saccade adaptation. Several studies showed that human eye



**Fig. 4** Influence of task-difficulty on saccade adaptation in [Schütz and Souto \(2015\)](#). (A) Perceptual performance in a fixation task as a function of retinal eccentricity. In the easy condition (gray), the gaps in the Landolt “Cs” were larger than in the difficult condition (black). Error bars represent 95% confidence intervals. (B) Magnitude of immediate adaptation. (C) Magnitude of gradual adaptation. (B and C) Small dots represent individual participants; large dots the mean across participants. Error bars represent 95% confidence intervals. *Redrawn from Schütz, A. C., & Souto, D. (2015). Perceptual task induces saccadic adaptation by target selection. Frontiers in Human Neuroscience, 9, 566.*

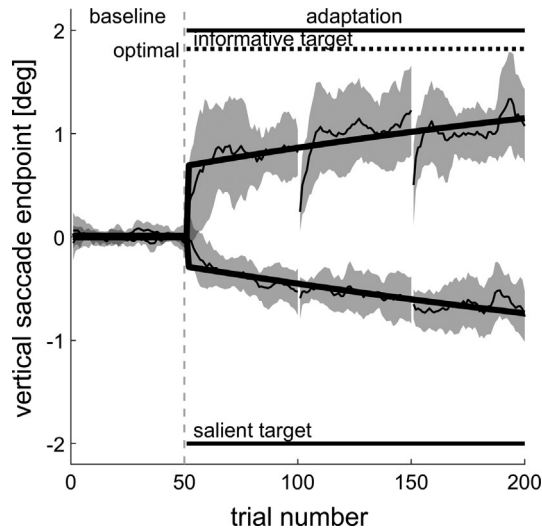
movement behavior in single trials is much less than optimal when two potential target locations need to be monitored and there is freedom to choose to fixate any point in-between the two locations ([Clarke & Hunt, 2016](#); [Morvan & Maloney, 2012](#)). Therefore, [Wolf et al. \(2019\)](#) set out to test if saccade adaptation can help observers to improve their eye movement behavior over several trials depending on relative informational gain.



**Fig. 5** Stimuli and double-target adaptation task to study the role of information gain for saccade adaptation in Wolf et al. (2019). Before the saccade, the informative and the salient target are overlaid. Upon saccade onset, both targets jump vertically in opposite directions. The informative target is characterized by low contrast and high-spatial frequency, such that it cannot be discriminated in the periphery. The salient target is characterized by high contrast and low-spatial frequency, such that it can be discriminated in the periphery. Adapted from Wolf, C., Wagner, I., & Schütz, A. C. (2019). *Competition between salience and informational value for saccade adaptation*. *Journal of Vision*, 19(14), 26, 1–24.

In a double-target adaptation paradigm, observers had to judge the orientation of two target stimuli (Fig. 5). Before the saccade, both stimuli are overlaid at the same location in the periphery. At saccade onset, the two targets split up and are shifted to a location either  $2^\circ$  above or below their initial location. Most importantly, a saccade to one of the two targets yields a high information gain, because the target's orientation can be identified only close to the fovea, whereas a saccade to the other target yields a low information gain, because the target's orientation can be identified already in the periphery. A model maximizing performance in the perceptual task, predicts that observers should adapt their saccade direction toward the target with high informational gain. Contrary to the model, the results show that adaptation direction depends crucially on the response order for the two targets: observers consistently adapt toward the target whose orientation they have to report first (Fig. 6). Most likely, there is a shift of visual attention after the saccade made toward the first target they have to report on, and this attention shift triggers adaptation. Instead of prioritizing the targets by their visibility, observers prioritize targets by response order. In doing so, they do not maximize their performance, since we know that they are more likely to be correct when the distance to the informative target is smaller.





**Fig. 6** Results in the double-target adaptation task in [Wolf et al. \(2019\)](#). In the first 50 trials, the informative and salient target were overlaid before and after the saccade. In the following 150 trials, targets split vertically after the saccade by  $2^\circ$  above and below the horizontal. The upper curve shows saccade amplitudes of observers who had to report the orientation of the informative target first, the lower curve shows saccade amplitudes of observers who had to report the orientation of the salient target first. The thin line represents the mean across observers, the shaded area 95% confidence intervals. The thick line represents the fits of the two-component model ([Section 5.2](#)). Redrawn from [Wolf, C., Wagner, I., & Schütz, A. C. \(2019\). Competition between salience and informational value for saccade adaptation. \*Journal of Vision\*, 19\(14\), 26, 1–24.](#)

In summary, we found clear effects of target prioritization in saccade adaptation, when two task-relevant targets compete with each other. This is further evidence for a top-down signal driving adaptation. However, the prioritization of targets is not exclusively determined by the information gain.



## 6. Neural substrates

The neural substrates of saccade adaptation in the double-step paradigm are relatively well-known, given the sophisticated understanding of visuo-oculomotor pathways, acquired mostly through single-cell recordings in the awake monkey (for reviews see [Fuchs, Kaneko, & Scudder, 1985](#); [Krauzlis, 2005](#); [Munoz, 2002](#); [Sparks, 2002](#); [White & Munoz, 2017](#)). Many studies have investigated how error signals are processed in the brain.

We will only briefly summarize the most important findings in that domain, for the sake of discussing candidate neural substrates of adaptation induced by top-down signals.

## 6.1 Adaptation by bottom-up error signals

The neuronal basis of adaptation driven by bottom-up error signals has been reviewed elsewhere (Iwamoto & Kaku, 2010; Prsa & Thier, 2011). The cerebellum has an important and general role in sensorimotor adaptation, specifically for the short-term changes that characterize saccade adaptation, and is responsible for adapting motor commands in response to visual errors. In the human, this picture might be more complex because saccade adaptation is less clearly motor, as there is also evidence of sensory adaptation (Hopp & Fuchs, 2004; Iwamoto & Kaku, 2010).

More specifically, lesions of the oculomotor vermis (OMV) and fastigial oculomotor region (FOR) in the cerebellum cause hypometria that remains uncorrected (Barash et al., 1999; Optican & Robinson, 1980) in the short-term. Signals from the superior colliculus (SC) carry information about visual errors to different regions of the OMV, where different locations show a preference for specific error directions (Iwamoto & Kaku, 2010). At the same time, every single Purkinje cell in the OMV receives inputs from regions of the SC representing all saccade vectors. The error signal to the Purkinje cells comes through the so-called climbing fibers originating in the SC and relaying in the inferior olive. Purkinje cells' output to FOR cells impacts premotor burst neurons and thereby adjust motor commands depending on the visual error.

The way Purkinje cells participate in motor learning may still be understood in light of the Marr-Albus theory (Marr, 1969; Albus, 1971; reviewed in Yamazaki & Lennon, 2019), positing that learning can be explained by synaptic plasticity (long-term depression) when the input from mossy fibers (a major input to the cerebellum) corresponding to a saccade vector and an error signal coming from climbing fibers are co-activated. Taking for instance a  $10^\circ$  saccade that overshoots the target and generates a  $3^\circ$  error: if signals from a mossy fiber coding for the saccade vector and the signal from a climbing fiber coding for a  $3^\circ$  error keep reaching the Purkinje cell at the same time they will cause long-term depression and ultimately a reduction of saccade amplitude (Iwamoto & Kaku, 2010). The pattern of the population response, depending on the error direction, determines the changes in saccade kinematics that differentially characterize forward and backward

adaptation in the monkey (Catz, Dicke, & Thier, 2008).<sup>c</sup> Therefore, one can think of Purkinje cells as a form of associative memory. FOR cells project to premotor nuclei in the brain stem (PPRF and riMLF) (Noda, Sugita, & Ikeda, 1990), which influence saccade kinematics for the purpose of maintaining accuracy (Herzfeld, Kojima, Soetedjo, & Shadmehr, 2015).

## 6.2 Adaptation by top-down signals: Beyond the cerebellum

The current knowledge of the physiology of top-down adaptation of saccades is only tentative compared to the vast amount of detailed investigations involving the cerebellum and subcortical structures. For instance, whereas there are many detailed single-cell physiological investigations of the role of cerebellar circuits on saccade adaptation, evidence for cortical implication is much sketchier and relying on more indirect methods (e.g., PET, TMS). Nonetheless, those studies have consistently pointed to neural pathways that could be implicated in top-down adaptation.

Several cortical “eye fields” are associated with top-down control of saccade eye movements (Pierrot-Deseilligny, Rivaud, Gaymard, Müri, & Vermersch, 1995). The frontal eye fields (FEF) and the posterior-parietal cortex (PPC; LIP in the monkey) have been implicated in the voluntary control of saccades, through their connections with the SC. Specifically, FEF has been implicated in target selection and voluntary control of saccades. Therefore, it could provide the necessary signal to support top-down adaptation by steering target selection (Blurton, Raabe, & Greenlee, 2012).

The study of Panouilleres et al. (2012) raises the possibility that the adaptation of voluntary saccades, unlike reactive saccades, relies more directly on the activation of the intraparietal sulcus (Panouilleres et al., 2012) since trans-cranial magnetic stimulation of this area reduced adaptation of voluntary saccades but not reactive saccades (Gerardin, Miquee, Urquizar, & Pelisson, 2012; Panouilleres et al., 2012). This difference between adaptation of voluntary and reactive saccades is also illustrated by differential transfer to antisaccades, in which observers need to invert the saccade vector and look opposite to the target’s side (Cotti et al., 2009).

Studies on patients with thalamic lesions (Gaymard, Rivaud-Péchoux, Yelnik, Pidoux, & Ploner, 2001; Zimmermann, Ostendorf, Ploner, &

<sup>c</sup> We must note that there is contradictory evidence about the presence of adaptation effects on saccade kinematics both in humans and non-human primates (e.g., Collins, Semroud, Orriols, & Dore-Mazars, 2008; Rahmouni & Madelain, 2019; Alahyane & Pelisson, 2005; Ethier et al., 2008a; Straube & Deubel, 1995); and more experimentation is needed to explain how the diverging results depend on experimental paradigms and data analysis (for a review see Pelisson et al., 2010).

Lappe, 2015) observed impairments in saccade adaptation, suggesting that an intact thalamic connection between frontal cortex and the cerebellum is necessary and emphasizing the crucial role of frontal cortex for saccade adaptation.

A link between saccade adaptation and the attentional network has also been recently unveiled through the analysis of magnetoencephalographic waveforms. Saccade adaptation was found to increase synchronization in the gamma-band (Nicolas et al., 2019), a range of temporal frequencies that has been associated with attentional processing. This again suggests a role of a cortical attentional network in specifying target selection driving saccade adaptation. One can link this proposal to the predictive coding framework we alluded to above, in which the allocation of visual attention is inextricably related to the processing of prediction errors (Smout et al., 2019; van Boxtel & Lu, 2013), which may be processed in the cortex. Accordingly, a number of cortical areas show activity correlated with retinal errors after inaccurate saccades (Guillaume, Fuller, Simal, & Curtis, 2018).

It is possible that subcortical and cerebellar mechanisms involved in saccade adaptation induced by the double-step paradigm remain the same with our top-down adaptation paradigm, which could explain the similarity in behavior with double-step adaptation. Even with the double-step paradigm, the nature of the error signal is actually not very clear (Iwamoto & Kaku, 2010). There is a possibility that top-down *and* bottom-up adaptation rely on similar error signals, as they both involve target selection. In one case, selection is determined by a cortical attentional network and in the other by a subcortical selection network, comprising the SC and being responsible for reflexive orienting (Fecteau & Munoz, 2005). In both cases, there is a misalignment between the focus of attention and the predicted location of the location to process (the perceptual target) after the saccade, which provides a teaching signal, which we may call a predictive selection error. This mismatch could be read out within SC, FEF or LIP after each saccade and conveyed to the cerebellum.



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## 7. Outstanding questions

Our review covers the current knowledge regarding the influence of top-down signals in driving saccade adaptation. We showed that target selection is an important error signal driving adaptation, which can under some conditions be dissociated from a bottom-up retinal or prediction error. There are a number of pending questions for future research.

We have seen that to some extent bottom-up and top-down driven saccade adaptation share astonishing similarities. However, bottom-up saccade adaptation in the double-step paradigm is defined by many more characteristics, such as its specificity to adapted saccade vectors (Noto et al., 1999; but see Rolfs et al., 2010) and initial eye position (Havermann, Zimmermann, & Lappe, 2011; Wulff et al., 2012). In addition, forward adaptation is typically slower compared to backward adaptation (e.g., Deubel et al., 1986; Rahmouni & Madelain, 2019) and those types of adaptation are believed to involve different correction mechanisms (Ethier et al., 2008a; Golla et al., 2008). Whether top-down driven saccade adaptation shares these characteristics is currently still unknown. If this were the case, we would have good evidence that similar error signals are corrected in both cases, as determined by top-down and bottom-up target selection.

We have seen that top-down adaptation may be intimately linked to the attentional system. If that is the case, the ability to select a target may be limited in capacity. For instance, we may then ask if it is possible to preserve different adaptation states for two different perceptual tasks. In a similar manner we may ask how the competition between those different error signals is resolved.

Research on visuomotor adaptation has clearly disentangled explicit from implicit and fast from slow learning processes and also addressed their interaction (for a review see Huberdeau, Krakauer, & Haith, 2015). Similar attempts haven't been made with respect to double-step saccade adaptation (Ethier, Zee, & Shadmehr, 2008b; van Es & Knapen, 2019), but the role of explicit and implicit processes for top-down saccade adaptation remains to be explored. In our investigations fast learning has been taken as a proxy of strategic learning, but we may ask, for instance, whether high cognitive load (e.g., induced by the presence of a demanding concurrent task) would reduce this learning component, or not.

Finally, there is no clear picture about what can form the neural substrates of top-down adaptation. Understanding how the error driving adaptation is derived is essential to determine whether top-down and bottom-up adaptation rely on a similar circuitry. One proposal could be that the corrected error is a predictive selection error, as resulting from the misalignment of the task-relevant information that is predicted to be available after the saccade and its actual location. Target selection itself might be determined by various bottom-up and top-down signals converging in the SC, opening saccade adaptation to influences such as reward or informational gain.



## 8. Conclusions

There is evidence that task-relevance not only exerts top-down modulation of adaptation, but it is also able to drive adaptation with similar characteristics to bottom-up driven adaptation in the double-step paradigm. This finding is consistent with an integrated view of the saccade system, where bottom-up and top-down signals converge to define the saccade target and the orienting of attention. Saccade adaptation might be a more general mechanism than previously thought. It does not simply correct internal errors within the visuomotor system, but more generally optimizes eye movements with respect to external factors, such as information gain and their relevance as determined by interactions with the environment. We pointed out possible neural substrates of top-down adaptation, which largely remains to be elucidated in contrast to the detailed experimental and modeling work linking the cerebellum to bottom-up driven adaptation in the double-step paradigm.

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