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Perisaccadic remapping: What? How? Why?

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Abstract: About 25 years ago, the discovery of receptive field (RF) remapping in the parietal cortex of nonhuman primates revealed that visual RFs, widely assumed to have a fixed retinotopic organization, can change position before every saccade. Measuring such changes can be deceptively difficult. As a result, studies that followed have generated a fascinating but somewhat confusing picture of the phenomenon. In this review, we describe how observations of RF remapping depend on the spatial and temporal sampling of visual RFs and saccade directions. Further, we summarize some of the theories of how remapping might occur in neural circuitry. Finally, based on neurophysiological and psychophysical observations, we discuss the ways in which remapping information might facilitate computations in downstream brain areas.

Keywords: cortex; perception; remapping; saccade; vision.

Introduction

The concept of the receptive field (RF) is one of the central principles of sensory neuroscience. First quantitatively described by Hartline (1941) in the retinal ganglion cells of frogs, the RF of a visual neuron is a spatial region within which sensory stimuli can elicit a neural response. In the visual system, neurons are typically arranged so that nearby neurons have RFs that encode similar spatial locations (Hubel and Wiesel, 1965); this is the basis of retinotopic organization in the visual cortex.

We make several saccadic eye movements every second as we scan the visual scene around us; as a result, the visual input is constantly being shifted in retinotopic space. Yet, 'when we turn about, the whole optical space appears to us a continuity and not an aggregation of fields of vision and … at the same time, the optical objects remain stationary …' in the words of Mach (1897). There must be a way for the brain to compensate for these self-generated movements while processing the visual input to construct a stable and seamless percept. Theoretical and experimental studies attribute this compensation to an integration of visual inputs with motor signals that encode eye position and movement parameters as well as head position and other nonvisual inputs (Judge et al., 1980; Galletti et al., 1993; Sommer and Wurtz, 2008; Wurtz, 2008; Sun and Goldberg, 2016).

The integration of visual and motor signals has been the focus of numerous studies. Retinotopic representations are most clearly found in early visual cortex, whereas oculomotor signals are clearly apparent in parietal and frontal cortices (Wurtz and Mohler, 1976a; Galletti et al., 1993). However, oculomotor influences have also been found throughout the visual system (Wurtz, 1968; Fischer and Boch, 1981; Nakamura and Colby, 2002; Reppas et al., 2002). The nature of these influences has variously been shown to be a suppression of some visual input (Burr et al., 1994; Thiele et al., 2002; but see Dorr and Bex, 2013), a facilitation of other kinds of input (Moore, 1999; Reppas et al., 2002), a distortion of visual space (Ross et al., 1997; Krekelberg et al., 2003; Richard et al., 2009, 2011), and a shifting of visual RFs before a saccade (Mays and Sparks, 1980; Duhamel et al., 1992; Yao et al., 2016b; Neupane et al., 2016a, 2017). This latter phenomenon has been called RF remapping and is the focus of this review.

Recent reviews of remapping have focused on its anatomical basis (Rao et al., 2016) and possible functional implications (Wurtz, 2008; Wurtz et al., 2011; Wurtz, 2015, 2018; Sun and Goldberg, 2016). Although we touch on these issues here, our focus is on the properties of remapping, the challenges associated with studying them and a potential functional role for remapping in the brain.

Early studies

RF remapping is typically thought to be linked to corollary discharge signals – these are copies of motor commands that are sent to sensory areas around the time of movement execution. Helmholtz, Mach, and Herring discussed corollary discharges using different terms, such as 'will' and 'sense of self', but the term 'corollary discharge'

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(Sperry, 1950) [and the related concept of 'efference copy' (Von Holst and Mittelstaedt, 1950)] has gained wide acceptance.

Indirect evidence of the influence of corollary discharge signals on visual perception emerged from John Stevens's paralysis experiment. Stevens et al. (1976) used curare to paralyze themselves while remaining fully conscious. They documented their perception while attempting to move their eyes. Every attempt to move the eye was followed by a perceived displacement of the visual scene in the direction of the attempted eye movement. The participants described this experience of displacement as 'not typically visual in nature' and had difficulty in conveying its character. Because this perception of displacement required an attempt to contract the eye muscles, it was thought to be associated with a corollary discharge of the oculomotor command.

Although such qualitative visuomotor links were emerging, there was significant progress being made in understanding the organization and architecture of the mammalian visual and oculomotor systems. The concept of the RF and its retinotopic organization in the neocortex was established early (Hartline, 1941; Hubel and Wiesel, 1977). At the same time, oculomotor researchers were documenting the properties of visuomotor neurons located in different areas of the primate brain, such as the superior colliculus (SC; Goldberg and Wurtz, 1972a; Mays and Sparks, 1980), the lateral intraparietal area (LIP; Goldberg et al., 1990), and the frontal eye fields (FEF; Mohler et al., 1973).

Fischer and Boch (1981) studied neurons in the prelunate gyrus (later identified as visual cortical area V4) in monkeys trained to execute saccades to visual targets. They found that neurons in this area often responded to stimuli placed near the saccade target when the animal was planning a saccade. The authors called these transiently modulated RFs 'goal fields' (Fischer and Boch, 1981, their Figure 2), as they were centered on the saccade goal. A neuron's goal field was typically larger than its RF and contained the RF, but it was not yet clear whether the goal field was simply a modulation of the existing RF or a shift in the spatial position of the RF (Fischer and Boch, 1981).

At the same time, experiments from the Wurtz laboratory examined the visual RFs of neurons in SC and also in monkeys trained to make visually guided saccades. The results were in some ways similar to those found by Fischer and Boch (1981); neurons in the superficial layers of SC showed larger responses when saccades were made close to their RFs (Goldberg and Wurtz, 1972b; Wurtz and Mohler, 1976b). This 'presaccadic enhancement' was accompanied by an expansion of the RF size in a fraction of SC neurons (Goldberg and Wurtz, 1972b). Similar results were obtained in FEF neurons (Wurtz and Mohler, 1976a; Bruce et al., 1985), but little or no enhancement was found in the primary visual cortex (Wurtz and Mohler, 1976a).

Saccades are a type of overt orienting of attention, in which the axis of gaze is pointed at an object of interest. However, attention can be deployed in the absence of a saccade, in which case it is called covert attention; shifts in covert attention are in some ways similar to overt saccades (Goldberg and Wurtz, 1972b; Fischer and Boch, 1981). In area V4, neuronal responses were found to show enhancement when covert attention was shifted to their RFs (Moran and Desimone, 1985). Similar enhancement occurred in the posterior parietal cortex when saccades were made to an RF stimulus or when covert attention was maintained over it (Bushnell et al., 1981).

These early results showed a modulation of the responses to stimuli in the RF by covert or overt attention. In contrast, Mays and Sparks (1980) reported SC neurons that responded during a saccade task to visual probes presented outside their classical RF. They used a double-step saccade task (Figure 1) in which monkeys were rewarded for making two consecutive saccades to targets flashed sequentially at two locations, O and B, while recording from a neuron whose RF was initially at location A. As the trial started with fixation at O, the monkey had to make the first saccade to B and the second saccade back to O. In this configuration, the target of the second saccade (location O) became the location of the RF (marked 'FF' for future field) after the completion of the first saccade. Although

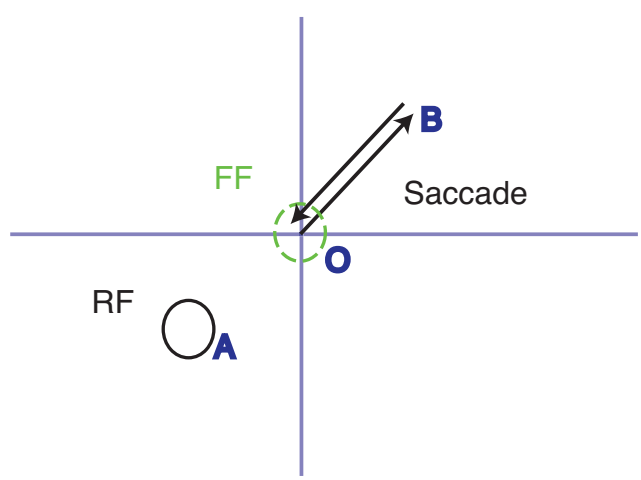

Figure 1: Double-step saccade task used by Mays and Sparks (1980), which led to the discovery of 'quasi-visual cells'. A represents the RF of SC neuron under study. Monkeys were rewarded for making two consecutive saccades, first to a briefly flashed target at B and second saccade back to the original fixation point at O. B was chosen such that the RF would fall at position O after the first saccade.

the target flashes were extinguished before (the first) saccade onset, some neurons responded presaccadically as though a visual stimulus was present in its RF (Mays and Sparks, 1980, their Figure 7D). This was surprising, as the neurons' responses seemed predictive of an upcoming saccade. They called these neurons 'quasi-visual cells', as they were neither movement neurons nor purely visual. Subsequently, some neurons in the LIP showed similar predictive properties in a similar double-step saccade task (Goldberg and Bruce, 1990, their Figure 6).

These early results suggested that RFs are not always fixed in retinotopic space. This was demonstrated dramatically in a landmark experiment carried out by Duhamel et al. (1992). They showed that neurons in LIP responded to visual probes outside their classical RFs, in their postsaccadic RFs, even when no second saccade was planned, implying a transient shift of the RF to its postsaccadic location before the saccade onset (Duhamel et al., 1992, their Figure 3C). As mentioned above, the shift from the RF to its future location (FF) was termed RF remapping.

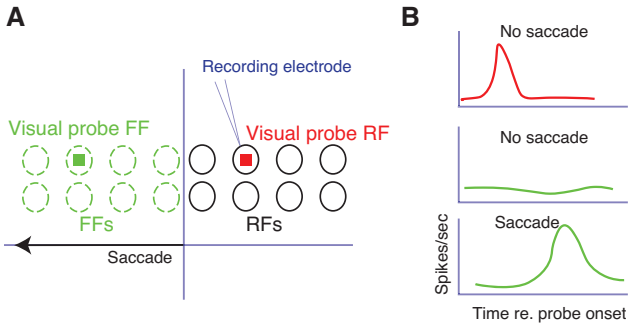

Figure 2: Illustration of RF remapping.
(Left) A hypothetical arrangement of visual RF tiling the visual field. During fixation, a neuron responds to a visual stimulus in its RF (orange; right, top trace) but not to a stimulus outside its RF (red; right, middle trace). When a rightward saccade is planned, we can define an FF, which is the position the RF will occupy after the saccade. Many neurons will respond to FF stimuli in this case, leading to the phenomenon known as RF remapping (red; right, bottom trace).

Recent studies

The crucial experiment done by Goldberg et al. made use of a rather simple experimental paradigm: the subject was cued to make a saccade, and in the interval between the appearance of the cue and the execution of the saccade (typically ~200 ms), a brief visual stimulus was flashed and extinguished. Neurons in LIP never responded to visual stimuli flashed outside the RF during passive fixation, but they frequently responded to probes in the same retinal positions if the animals were planning a saccade in the appropriate direction (see Figure 2 for a cartoon illustration). Using similar paradigms, this finding was replicated in LIP (Heiser and Colby, 2006; Wang et al., 2016) and across several other cortical areas, such as FEF (Umeno and Goldberg, 1997, 2001; Kusunoki and Goldberg, 2003; Sommer and Wurtz, 2006), V3, V3A (Nakamura and Colby, 2002), V4 (Neupane et al., 2016a,b, 2017), medial superior temporal (MST; Inaba and Kawano, 2014), and SC (Walker et al., 1995; Churan et al., 2011). Moreover, after sophisticated electrophysiological studies in alert monkey, it was found that remapping in the FEF is triggered by a corollary discharge signal that originates in SC and ascends to the frontal cortex via the medial dorsal nucleus of the thalamus (Sommer and Wurtz, 2002, 2006).

It is noteworthy that the presaccadic target-related enhancement observed by Fischer and Boch (1981) and Wurtz et al. (described above) could also be interpreted as a perisaccadic RF shift. In this case, the shift would be toward the saccade target because of the enhanced responses found in that part of visual space. Such a shift is quite different from the classic RF to FF remapping effect described above. To explore this type of remapping, Tolias et al. (2001) assessed the spatial structure of perisaccadic RFs in area V4 of the monkey visual cortex by presenting stimuli at various positions throughout the visual field around the time of a saccade. As predicted from presaccadic enhancement, the results showed that some V4 RFs transiently converged toward the saccade target rather than toward the future RF position (Tolias et al., 2001). A similar conclusion was reached in a study of FEF neurons by Zirnsak et al. (2014). More recently, we have shown, in V4 neurons, that both types of RF shifts can be observed depending on the timing of the responses and the saccade vector (Neupane et al., 2016a, 2016b). Similar results have been recently reported in the middle temporal (MT) area as well (Niknam et al., 2019).

Based on these findings, it has been suggested that there are two types of remapping: a shift of the RF toward its FF, called forward remapping (Marino and Mazer, 2016), and a shift toward the saccade target, called convergent remapping (Marino and Mazer, 2016). These ideas are not incompatible, and it can be argued that one is a special case of the other (Sommer and Wurtz, 2006; Zirnsak and Moore, 2014). As outlined below, we suggest that different experimental designs will naturally emphasize one or the other type of phenomenon. It is rather challenging in any one experimental setting to completely document the effects of saccades on visual RFs.

Perisaccadic influences on visual RFs

The abovementioned studies have made it clear that visual RFs are not fixed in retinal coordinates. In fact, visual responses during saccades depend in a rather complex way on visual stimuli and the saccade target and other contextual factors such as the structure of the visual scene. Most previous studies have examined a limited number of these influences, and so our picture of RF remapping remains somewhat fragmented.

In this section, we discuss forward and convergent remapping and other perisaccadic influences on visual RFs as well as some technical considerations that might facilitate future efforts at capturing perisaccadic RF changes.

Space

Remapping is fundamentally a change in the spatial position of an RF that is triggered by a saccade. Given this definition, it is important to characterize the spatial structure of RFs with resolution sufficient to distinguish remapping from other kinds of perisaccadic influences. As mapping of RFs requires tens of trials at multiple spatial locations, a remapping experiment demands many saccade trials.

Given the multiplicity of possible responses mentioned above, it is critical to distinguish three sources of possible response modulation. The first is the standard retinotopic RF, which we call the current field. The second is the position that would be occupied by the RF in the event of forward remapping; this is the FF, whose position depends on the saccade vector. Finally, there is the zone of presaccadic enhancement, which will always be centered on the saccade target. As mentioned above, even something as simple as presaccadic enhancement can lead to changes in the spatial structure of RFs, as weak responses in the periphery during fixation become easier to detect around the time of a saccade.

To disentangle these influences, one must, at a minimum, probe spatial locations intermediate between current and future RFs, as the enhancement effects reported previously in SC could otherwise be mistaken for forward remapping. A few studies that have made use of intermediate probes in the FEF (Umeno and Goldberg, 2001; Sommer and Wurtz, 2006) and SC (Churan et al., 2012a) have found evidence consistent with forward remapping: perisaccadic responses were stronger when the probes were placed closer to the FF and farther from the current field.

In addition to probing visual responses along the direction parallel to the saccade, it is important to probe orthogonal directions as well to detect RFs shift toward the saccade target (Tolias et al., 2001; Sommer and Wurtz, 2006; Zirnsak et al., 2014; Neupane et al., 2016a; Hartmann et al., 2017). Such shifts can masquerade as forward remapping when a small number of positions are probed (Figure 3; Zirnsak et al., 2014). The need to probe spatial locations both parallel and orthogonal to the saccade vector highlights the importance of using a range of locations chosen to span the range of hypothesized RF positions (current field, FF, and saccade target).

However, even a careful probing of spatial locations can be insufficient to reveal the full picture of RF remapping, as the relationship between the spatial and temporal structures of a remapped RF is not independent. Wang et al. (2016) have shown that LIP neurons remap from their fixation RF to their FFs by shifting along a trajectory parallel to the saccade vector. Similarly, the relative strength of forward and convergent remapping can vary through time (Neupane et al., 2016a). These dynamics highlights the need to sample both space and time as finely as possible.

Time

The strength of remapping varies with the time of stimulus presentation relative to saccade onset (Kusunoki and Goldberg, 2003), and it has been suggested that responses observed at different times reflect distinct phenomena (Umeno and Goldberg, 1997, 2001). Specifically, when the probe is flashed long before the saccade, one can detect what is called ‘predictive remapping’ (Sun and Goldberg, 2016), a type of forward remapping in which the RF moves to its postsaccadic position in advance of the saccade. This has most often been

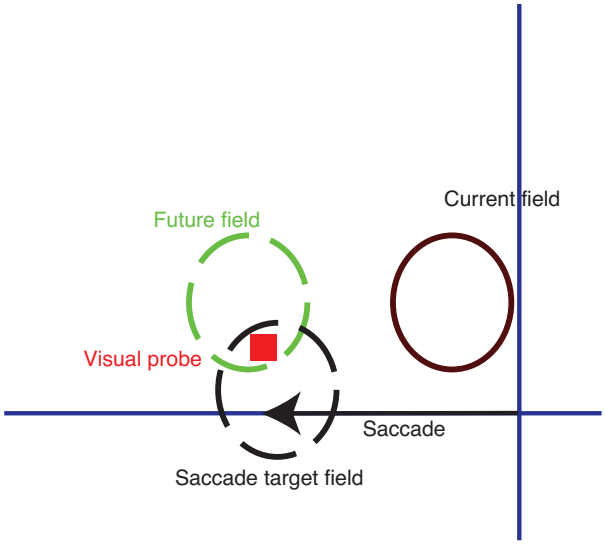

Figure 3: Future RF confounded by an overlapping saccade target field.

reported in oculomotor areas such as SC, FEF, and LIP (Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg, 1997) as well as parts of the extrastriate cortex (Nakamura and Colby, 2002). Note that these studies did not probe the spatial structure of RFs at high resolution, so there remains a question about the relative strength of convergent and forward remapping during the presaccadic period.

When the probe is flashed closer to saccade onset, there is often an observation of what is called 'memory remapping' (Umeno and Goldberg, 2001), a type of forward remapping in which the remapped response occurs long after the saccade is complete (Umeno and Goldberg, 2001; Churan et al., 2011; Neupane et al., 2016a). Often, these memory responses exhibit latencies that are substantially longer than visual responses, and they can sometimes persist for many seconds, even extending across intervening trials (Umeno and Goldberg, 2001; Semework et al., 2018). Memory remapping has been observed in V4 (Neupane et al., 2016a), SC (Walker et al., 1995; Churan et al., 2011), MST (Inaba and Kawano, 2014), and FEF (Umeno and Goldberg, 2001).

In area V4, there is strong convergent remapping during the presaccadic period when saccades are directed close to the RFs (Tolias et al., 2001; Neupane et al., 2013; Hartmann et al., 2017). This effect starts 100–50 ms before the saccade and lasts until 50 ms after the saccade (Tolias et al., 2001). It strongly resembles the presaccadic enhancement reported by Fischer and Boch (1981a) in both its time course and its dependence on the saccade vector (see below for more details). Neupane et al. (2016b) also reported a type of convergent remapping that occurred with a very long latency. For stimuli flashed just before the saccade, RFs remapped toward the saccade target, but such responses were often not evident until 300 ms after the saccade. However, further testing revealed that similar responses could be observed during steady fixation, provided that the subjects were anticipating the execution of a saccade in the corresponding direction (Neupane et al., 2016a, their Figures 4 and 5). This type of convergent remapping can therefore be explained as a side effect of covert attention directed toward the saccade target. Indeed, previous work has shown that attentional modulation can shift the positions of RFs in V4 (Connor et al., 1996) and MT (Womelsdorf et al., 2006), with a sluggish time course (Hayden and Gallant, 2005) and without any eye movement. These results suggest that attention shifts can lead to a complex pattern of RF effects, particularly in experimental paradigms in which attention is not explicitly controlled.

Saccade vector

We have suggested (Neupane et al., 2016a) that the previous pattern of results can be explained as a manifestation of two processes, both active around the time of a saccade. The first process is a shift of attention toward the saccade target, which can enhance the responses to stimuli presented near the saccade target (Fischer and Boch, 1981; Hamker et al., 2008; Zirnsak et al., 2014). For RFs that are sufficiently close to the saccade target, this attentional effect will appear as presaccadic enhancement, which will shift the envelope of the RF toward the saccade target. Computational models based on this principle provide a plausible explanation for the data on convergent remapping (Hamker et al., 2008).

Because these enhancement effects decline with distance from the saccade target (Fischer and Boch, 1981; Tolias et al., 2001), a second process is necessary to account for forward remapping, which is observed even for saccades made into the visual hemifield opposite the RF (Heiser and Colby, 2006; Churan et al., 2011; Neupane et al., 2016a). Thus, a parsimonious account of perisaccadic RF changes would include an enhancement effect localized to the vicinity of the saccade target (Hamker et al., 2008) and a remapping that is similar across all of visual space (Heiser and Colby, 2006; Mirpour and Bisley, 2012; Neupane et al., 2016a).

Even this simple account can lead to complex observations, as the relative strengths of the two types of remapping are likely different in different brain regions. They are also likely to have different time courses, depending on a number of experimental factors, as discussed above. Given these considerations, it is essential for experimentalists to choose saccade vectors that will isolate the effect of interest for a given study. Saccades directed close to the center of a neuron's RF will emphasize attentional effects such as convergent remapping, whereas saccades directed far from the RF center provide an opportunity to detect forward remapping. However, notions of 'near' and 'far' can be confounded by the brain's representation of visual space, which is distorted by the cortical magnification factor (Hamker et al., 2008; Richard et al., 2009). Another approach is to choose saccade vectors that dissociate the two types of remapping (Zirnsak et al., 2014; Neupane et al., 2016a; Hartmann et al., 2017). This was achieved in our recent study that placed the saccade target in the direction of the RF under study but only half the distance to the RF from the fovea (Neupane et al., 2016b). The angle between forward and convergent remapping in such a scenario is close to 180°, as shown by Neupane et al. (2016b, their Figure 1),

thus largely minimizing any spatial overlap between the two types of remapping. The V4 neurons predominantly exhibited forward remapping under these conditions (Neupane et al., 2016b).

Yet another approach is to use saccades directed into the hemifield opposite the RFs, exploiting the fact that retinotopic mapping is strictly contralateral in most visual structures. This approach thus avoids the possibility of accidently stimulating the fringe of the RF with probes placed near the saccade target. Previous studies have shown that convergent remapping is dependent on the geometry of the saccade relative to the RF location (Tolias et al., 2001; Hartmann et al., 2017) and is largely diminished for saccades directed away from the RFs (Tolias et al., 2001; Neupane et al., 2016a). This makes sense, as spatial attention during saccades is typically localized to the saccade target (Deubel and Schneider, 1996), so that presaccadic enhancement is largely confined to the hemifield containing the RF (Moore et al., 1998). Thus, saccades directed away from the RFs likely provide a purer measure of forward remapping.

Contextual effects

Early studies of remapping made use of visual probes presented against a dark background (Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg, 1997). Churan et al. (2011) replicated this phenomenon in SC, but their results showed that remapping was much weaker when probes were presented against a lit background. The different background conditions were interleaved, precluding any adaptation effects. These results suggest that forward remapping occurs most commonly under conditions in which it is likely to be useful. That is, if the goal is to localize objects in visual space across saccades, it can be argued that one should keep track of object positions relative to visible landmarks, as these relationships do not change with saccades (Deubel et al., 2010). In darkness, such information is not available, and the use of corollary discharges becomes essential. A related point is that neither forward nor convergent remapping is observed in the absence of a salient visual probe stimulus. In particular, when many probes are presented simultaneously, RFs remain stable in retinal coordinates throughout the execution of the saccade and afterwards in SC (Churan et al., 2011, 2012b), V4 (Zanos et al., 2015, 2016; Marino and Mazer, 2018), and FEF (Joiner et al., 2011). Thus, importantly, remapping depends on the stimulus context.

These results can be interpreted within the theory of attentional pointer remapping (Cavanagh et al., 2010). This theory argues that the brain remaps stimuli, which are selected by spatial attention. The rest of the locations need not be maintained under spatial stability, as the subject is inattentive to and hence unaware of them anyway. This account provides an explanation of the abovementioned contextual effects, which show that remapping occurs only for salient stimuli that attract bottom-up attention (Churan et al., 2011; Joiner et al., 2011). Recent experiments in which top-down attention was controlled provide strong confirmation of this theory (Yao et al., 2016a).

Closely related to the notion of attentional pointers is the possibility that remapping reflects a reflexive shift of the oculomotor plan toward the stimulus probe. That is, animals might automatically plan a saccade toward the probe, which is never executed but which nevertheless might elicit a response in some brain structures. Indeed, the quasi-visual cells described in SC by Mays and Sparks (1980) and the tonic neurons described by Walker et al. (1995, their Figure 15B) respond to a presaccadic FF stimulus if there is an impending second saccade to the stimulus. On this basis, one could expect a response from some neurons to a stimulus in the FF, even without a saccade. Umeno and Goldberg (2001) tested this idea by having animals execute a series of saccades in which each target was located far from the FF probe. Despite the dissociation between the oculomotor plan and the stimulus probe, remapping responses were still observed in the FEF. Similar results were obtained by Tian et al. (2000); however, the same study showed that the FEF can maintain multiple saccade plans simultaneously, so this idea cannot be completely ruled out. Indeed, the long latency and small amplitude of remapping responses in some structures (Umeno and Goldberg, 2001; Neupane et al., 2016a) are consistent with the notion of a reflexive motor response that is insufficient to trigger an actual saccade.

A brief aside on technical considerations

Paradigm

The above considerations highlight the need for a paradigm that can capture RF dynamics in space and time relative to saccades. Recent studies (Zirnsak et al., 2014; Neupane et al., 2016a; Szinte et al., 2018) have begun using variations

of the remapping paradigm that make use of a probe grid encompassing the current field, FF, and fixation and saccade targets (Figure 4). On each trial, three probes are randomly chosen from all possible locations and flashed at various times relative to the saccade. Two probes (P1 and P3) are flashed long before (500–1000 ms) and long after the saccade to measure activity during fixation, and a presaccadic probe (P2) is flashed immediately before the saccade (50–100 ms) to measure perisaccadic activity. As only one location is probed every time one of these probes is flashed, data from all the trials are combined to obtain RF maps during fixation and around the time of a saccade. For a probe grid with 100 locations, a session of 2000 saccade trials typically yields a workable data set. This has proven to be a fruitful paradigm for visuomotor research with new studies adopting this approach (Szinte et al., 2018), although, as detailed below, some improvements are possible.

Display technologies

Most remapping experiments make use of a flashed stimulus that disappears before the onset of the saccade. This sort of stimulus provides an instantaneous picture of the oculomotor input as it alters RF responses during the perisaccadic interval. Previous work has found that this signal is most effective for stimuli presented near saccade onset (Kusunoki and Goldberg, 2003; Wang et al., 2016). Thus, examination of the properties of remapping requires that the probe stimulus should appear and disappear as abruptly as possible, so that the timing of the signal can be related precisely to that of the neural response.

Most of the early remapping studies were performed using visual stimuli directly produced by light-emitting diodes (LEDs) and projected onto a screen (Walker et al., 1995; Umeno and Goldberg, 2001). LEDs have very fast rise and fall times (on the order of microseconds), which makes them a safe choice of display technology to test remapping. However, these displays provide less flexibility than modern computer screens, and as a result, the earlier work generally did not sample enough spatial positions to thoroughly map RFs through time.

Among computer displays, cathode ray tube (CRT) displays have traditionally been considered the gold standard for generating precisely timed signals. Most CRTs exhibit very fast rise times (on the order of 1 ms or less), with decay times that can be somewhat longer, depending on the properties of the phosphor. This asymmetry means that a dark stimulus probe on a bright background decays faster than a bright stimulus probe on a dark background (Lagroix et al., 2012). Although the latter can generate misleading results in experiments requiring high temporal precision (Jonides et al., 1982; Irwin et al., 1983), the results on forward remapping that have been obtained with CRTs do not differ in any obvious way between dark and bright probes (Neupane et al., 2016a), nor do they differ from those obtained in the same paradigms with LEDs (Inaba and Kawano, 2014; Neupane et al., 2016b, 2017). Nevertheless, it is difficult to avoid this limitation entirely.

More recently, a number of display technologies exhibiting outstanding temporal properties have entered the market. In particular, commercially available monitors making use of LED display technology afford the precise control of stimulus onsets and offsets, with little evidence of persistence beyond the stimulus duration (Lagroix et al., 2012). Unfortunately, the majority of these devices are marketed as computer monitors, and as such, they have relatively small display areas, rendering them problematic for experiments that require RF mapping at large eccentricities.

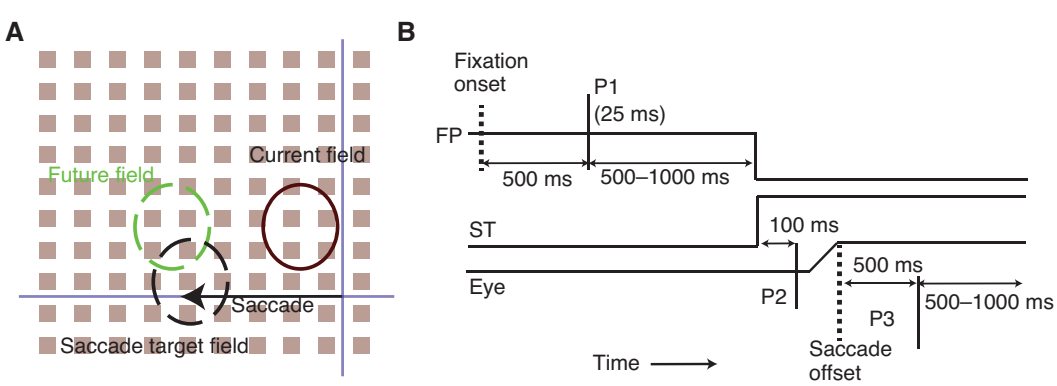

Figure 4: Remapping paradigm to probe all potential locations of the remapped RF.
(Left) Probe grid shown in faint red that encompasses an entire quadrant of left visual hemifield. A hypothetical neuron's RF (current field), FF, and saccade target field are represented by labeled circles. (Right) Time course of the experimental paradigm adopted by multiple studies, where P1 and P3 probes are used to map RFs long before and long after a saccade and P2 probe is used to map perisaccadic RF.

In contrast, LED televisions often have very large fields of view, making them useful for RF mapping experiments. We have tested one of these devices (Toshiba model #65l350U) using a paradigm that dissociates forward and convergent remapping (Neupane et al., 2016b). These devices do indeed have excellent temporal precision, and the results are similar to what we have reported previously (Neupane et al., 2016b).

Perhaps the most promising new technology is the organic LED (OLED), which provides extremely precise control of stimulus timing, contrast, and black levels (Cooper et al., 2013). OLED televisions with large screens are also available, and we have tested one of these devices (LG model #55EC9300) in V4 experiments on forward remapping (Neupane et al., 2017, their Figure 1B).

Overall LED and OLED televisions can be well suited for remapping experiments, but they have some rather frustrating limitations. Specifically, because they are manufactured primarily as televisions, they contain onboard image processing hardware and software that alters the contrast and luminance of the display depending on ambient light and content of display. These can be overcome to some degree; however, despite much effort on our part, we have not been able to disable them entirely. As a result, these displays generally exhibit long (though deterministic) input lags on the order of tens of milliseconds. This is not necessarily a problem, as long as the display system is carefully calibrated with the eye tracking system.

A complete solution is to purchase a projector with LED display technology, in which the onboard image processing features are absent or disabled. A few companies market such display systems specifically for vision research: the Propixx projector (Vpixx), the DepthQ (Cambridge), and the Light Engine (Dli) are examples. These devices are extremely expensive ($10,000–$40,000 as of this writing).

RF mapping algorithms

In the field of visual neuroscience, the problem of mapping an RF in space and time has been addressed by the development of increasingly sophisticated system identification techniques. As a result, it is now possible to map RFs in such a way as to capture even highly nonlinear or nonstationary aspects of a neuron's selectivity (Gallant et al., 1996; Mineault et al., 2012; Akbarian et al., 2017; Niknam et al., 2019).

Various groups have attempted to apply these tools to characterize RFs during eye movements. In the lateral geniculate nucleus (LGN), Reppas et al. (2002) used full-field luminance modulation to recover the temporal responses of neurons; they were able to show that LGN neurons are suppressed during the execution of a saccade. Later studies used spatiotemporal noise stimuli to capture RF changes during saccades in SC (Churan et al., 2011, 2012b) and visual cortex (Krekelberg et al., 2003; McFarland et al., 2015; Zanos et al., 2016). Although these studies revealed consistent changes in the temporal structure of visual responses during saccades, they largely failed to recover changes in RF positions. This is likely due in part to the contextual effects mentioned above, as remapping is far weaker for spatiotemporally dense stimuli.

The spatiotemporal noise stimuli used in these studies are useful for probing RFs in an assumption-free manner. However, they are relatively inefficient, as most neurons do not respond to most of the stimuli presented; this is particularly problematic as the pace of saccade execution sharply limits the amount of data that can be collected and hence the power of the RF models that can be recovered. A more fruitful approach might be to design stimuli and analysis methods that are optimized to test particular hypotheses about remapping. This would entail stimuli that are effective at eliciting responses in the area under study (rather than simply using square-shaped probes) and more modern parametric models that reduce RFs to a tractable number of parameters. Importantly, these models work well with naturalistic stimuli (Paninski, 2004; David and Gallant, 2005; Mineault et al., 2012; Cui et al., 2013), permitting an examination of hypotheses about the functional utility of remapping (see below).

How does remapping occur?

Although the anatomical pathways underlying the putative origin and transmission of the remapping signal have been identified (Sommer and Wurtz, 2006), the neural mechanisms that support remapping are unknown.

Integration of visual and oculomotor signals

As mentioned above, the observation of remapping has historically been related to the notion of a corollary discharge signal, which is a copy of the command to execute an eye movement. The advantage of this signal is that it is likely fast enough to be compatible with the timing of remapping. Recently, a model was proposed along with

physiological evidence from LIP neurons (Wang et al., 2016), in which the corollary discharge signal carries a dynamically updated copy of activity on the motor map of SC during saccades. It has previously been shown that a saccade is accompanied by a wave of activity from the caudal region of SC encoding the saccade target to the rostral part of SC in cats (Guitton, 1992) and monkeys (Munoz and Wurtz, 1995; Choi and Guitton, 2009). Wang et al. (2016) have proposed a model in which a corollary discharge of the activity in SC facilitates remapping, which travels across the retinotopic map of LIP along the trajectory defined by the saccade vector. Although the model proposes a simple mechanism for predictive remapping, the late memory remapping observed in other cortical areas are not temporally compatible with the timing of a moving wave of activity in LIP or SC, especially because the time constant of the memory remapping response can last for many seconds (Umeno and Goldberg, 2001; Semework et al., 2018).

Whereas the corollary discharge carries information about the change in eye position associated with each saccade, many brain regions also have access to information about the instantaneous eye position itself. In parietal cortex in particular, eye position signals are known to modulate visual signals multiplicatively through gain fields (Andersen and Mountcastle, 1983; Zipser and Andersen, 1988). Evidence for a role for eye position signals in remapping comes from several studies that have trained artificial neural networks to fit the properties of remapping (Xing and Andersen, 2000; Cassanello and Ferrera, 2007; Keith et al., 2010). Analysis of the hidden layer in these models points to the use of gain field-like signals. It has been previously shown that gain fields combine with retinotopic information to achieve spatial constancy in craniotopic coordinates (Zipser and Andersen, 1988; Salinas and Thier, 2000). Whereas gain field modulation is known to remain unreliable for up to 250 ms after a saccade (Morris et al., 2012; Xu et al., 2012), remapping can start as early as 50 ms before a saccade (Umeno and Goldberg, 1997). Therefore, the neural network-based models fail to capture the fast dynamics of remapping often observed in physiological data.

In contrast, the model of Wang et al. (2016) is particularly plausible, as it does not depend on the slow gain field signal (Morris et al., 2012; Xu et al., 2012). It has been suggested that proprioceptive signals from the eye muscles (Wang et al., 2007) might be the source of late memory remapping as well as that of the gain field signal (Sun and Goldberg, 2016). Therefore, a full model of remapping would combine both corollary discharge and proprioceptive signals. Indeed, such a multimodal scheme has been shown to play a role in localization of points in space when multiple sequential saccades are made in dark (Poletti et al., 2013).

Circuit mechanisms of remapping

Classically, visual RFs are thought to arise early in development to maintain their retinotopic topography throughout life (Wiesel and Hubel, 1963). In contrast, the phenomenon of RF remapping suggests that neurons can respond to visual stimulus placed anywhere on the retina depending on the momentary direction of a saccadic eye movement. This requires a mechanism for flexibly transferring information across retinotopic space. Along these lines, several circuit models have been proposed.

Quaia et al. (1998) proposed a model in which FEF movement neurons and LIP neurons encoding the FF are connected to the same LIP neuron encoding the current field. Remapping then occurs by the two inputs being multiplied at the dendritic level of the LIP neuron encoding the current field. The model proposes that the connection between these trio of neurons encoding corollary discharge, FF, and current field is learned through visual experience across multiple saccades (Quaia et al., 1998). The main challenge with this model is that the connectivity needs to represent all possible saccade vectors and be altered accurately and rapidly once a saccade is programmed. Additionally, the model only explains the transfer of location information of visual stimulus and not its features (Cavanagh et al., 2010).

A theory of remapping, which is behaviorally and computationally plausible, is that of attentional pointers (Cavanagh et al., 2010). According to this theory, forward remapping is not a literal shift of an RF but a transfer of activity pertinent to the attentional loci in the visual field at the moment of eye movement. This is behaviorally relevant because an object of attention is kept under the same spatial frame before and after an eye movement by the virtue of remapping of activity. It is also computationally parsimonious because not more than a few locations of interest have to be remapped as opposed to the entire visual field. Support for this model comes from the studies by Yao et al. (2016a), who showed that remapping does not occur for stimuli that are ignored by the subject (Yao et al., 2016b). This is also a prediction of the attentional pointer hypothesis. To the extent that this theory is correct, the circuits supporting remapping should be tightly linked to those that support attentional shifts. Although this idea has not been tested directly, the pathways for corollary discharge signals, including SC and FEF, are largely

overlapping with those for attention (Sommer and Wurtz, 2006; Berman and Wurtz, 2011; Krauzlis et al., 2013). In contrast, there is some evidence that oculomotor and attentional signals are segregated in the projections from FEF to visual cortex (Gregoriou et al., 2012), so the relationship between corollary discharge, attention, and remapping remains an open question.

More generally, there are several lines of previous work that have shown that flexible routing of information on short time scales can be achieved through the temporal alignment of neural oscillations (Buschman and Miller, 2007; Womelsdorf et al., 2007; Gregoriou et al., 2009; Bosman et al., 2012; Grothe et al., 2012; Saalmann et al., 2012), a mechanism also termed as 'communication through coherence' (Fries, 2015). The dynamic nature of this mechanism led us to hypothesize that it might subserve forward remapping in visual cortex, and we have tested this idea with multisite recordings in V4 (Neupane et al., 2017). We found that perisaccadic remapping in V4 is accompanied by an increase in the coherence of low-frequency alpha (8–12 Hz) local field potential oscillations between the sites encoding current and future RF locations. The coherence has properties similar to those of single-neuron remapping – it is modulated by visual stimulation at the FF and is specific to the saccade vector. The time scale of the oscillation is consistent with multiple lines of physiological evidence for thalamic involvement in relaying remapping signals from the brainstem to the cortex (Sommer and Wurtz, 2006; Cavanaugh et al., 2016). Thus, it is possible that the remapped information is temporarily stored elsewhere and brought back into the visual retinotopic map postsaccadically (Cavanagh et al., 2010), with alpha oscillations playing a role in holding the appropriately synchronized local retinotopic activity 'in-stock' (as suggested by Fries, 2015) to be subsequently combined with the remapped information. This mechanism provides an alternative means by which appropriate pairs of neurons on a retinotopic map can dynamically alter their functional connectivity during saccades (Bosman et al., 2012). However, it does not address the difficult problem of the underlying anatomical connectivity, which as in the Quaia et al. (1998) model must be capable of transferring information between arbitrary sites on a retinotopic map.

The mechanism of convergent remapping, in contrast, is thought to be a gain modulation of RFs by a top-down attentional signal (Hamker et al., 2008; Zirnsak et al., 2010). This, to date, is the most parsimonious model to explain the mechanism of convergent remapping. Here, a Gaussian RF is multiplied by an attentional component with a Gaussian profile centered at the saccade target. The product of the two Gaussians results in an RF whose center of mass is pulled toward the attentional field of activity centered at the saccade target causing an RF modulation observed in the convergent remapping neurons of FEF (Zirnsak et al., 2014).

Why does the brain use remapping?

Since the initial discovery of perisaccadic remapping (Duhamel et al., 1992), numerous studies have reported variations on the basic phenomenon, leading to a proliferation of terms and explanations. We have mentioned several categories of remapping – memory, predictive, convergent, forward – but others can be found in the literature. At the same time, the fragmentary nature of individual experiments suggests that some of these phenomena likely represent different ways of probing the same mechanisms. As mentioned above, studies of convergent remapping have generally undersampled saccade directions, whereas studies of forward remapping have undersampled space, and most studies have undersampled time. In this section, we try to synthesize these observations, although this exercise is necessarily limited by the fragmentary nature of the data.

To start with, it seems safe to say that saccades are accompanied by shifts of spatial attention (Deubel and Schneider, 1996; Deubel, 2008) and that shifts of spatial attention can alter the structure of visual RFs (Connor et al., 1997; Womelsdorf et al., 2006). These facts suggest that the phenomena of presaccadic enhancement (Fischer and Boch, 1981) and convergent remapping (Tolias et al., 2001) are manifestations of the deployment of spatial attention during saccades (Hamker et al., 2008). In this regard, it is important to consider that attention is often an uncontrolled experimental variable in remapping experiments, so that the precise extent of these influences can lead to unexpected neural effects (Neupane et al., 2016a) that depend on the experimental design and even on the subject's behavioral strategies. The behavioral consequences of attentional shifts during saccades have been thoroughly characterized: they include finer resolution of postsaccadic visual stimuli and enhanced target selection (Zirnsak and Moore, 2014).

Recent experiments have combined measurements of remapping with tight control of attention (Yao et al., 2016a, 2016b), and this, in our view, is an important advance. Indeed, previous results, as summarized above, suggest that only salient or attended stimuli are remapped (Churan et al., 2011; Joiner et al., 2011; Zanos et al., 2016). On this basis, one might conclude that remapping

is a subsidiary consequence of attention shifts (Hamker et al., 2008), but there are several observations that are incompatible with this view. Specifically, as attention is generally considered to act as a multiplicative gain on visual responses (McAdams and Maunsell, 1999), it should be ineffective when visual responses are very small (Treue and Martínez Trujillo, 1999). Nevertheless, forward remapping is observed for conditions in which the visual response is likely to be zero; examples include experiments in which remapping is observed several seconds after the stimulus has disappeared (Umeno and Goldberg, 2001; Semework et al., 2018) or when the stimulus is placed very far from the RF – in the opposite visual hemifield (Churan et al., 2011; Heiser and Colby, 2006; Neupane et al., 2016a). Although it remains possible that remapping entails an attentional modulation of visual responses that extend very far in space (Sundberg et al., 2009) and/or time (Funayama et al., 2015), a more parsimonious explanation is that attention is necessary but not sufficient to elicit remapping.

A space-time model

In this section, we attempt to relate neural data on remapping to observations on perisaccadic visual perception. For the neural data, we focus on the case in which saccades are directed away from the RFs of V4 neurons, a situation for which attentional influences are likely to be minimal (Connor et al., 1996). We also focus on forward remapping, as models of convergent remapping have been thoroughly developed in previous work by Hamker et al. (2008, 2011).

Our starting point is the notion of a space-time RF (Adelson and Bergen, 1985), which captures the spatial structure of visual responses and its dependence on the time of stimulus presentation. Given the considerations outlined above, these two factors (space and time) appear to be inseparable, so that there is a clear benefit to examining them together (Cicchini et al., 2013). A previous study has proposed a similar idea (Burr and Morrone, 2011).

To do this, we make use of reverse correlation: this is simply a description of the stimuli that, on average, were presented before the occurrence of a spike in a single neuron. Although we typically present stimuli across two spatial dimensions, we are interested here in a single dimension of space, namely the dimension parallel to the saccade vector. Thus, we map the RF in two dimensions and then plot its profile along a line that passes through the RF center and is parallel to the saccade vector (Figure 5A and B, dotted line). Plotting this slice at different time points yields the space-time map of the neuron's RF.

A space-time map for an example V4 neuron, measured during fixation, is shown in Figure 5C (same neuron from Neupane et al., 2016b, their Figure 1C). Whereas a typical peristimulus histogram would depict the probability that a neuron fires spikes for a given stimulus, in the framework of reverse correlation, we ask what stimulus was most likely given the occurrence of a spike. Therefore, for a spike fired at time 0 in Figure 5C, there was most often a stimulus flashed in a narrow range of spatial positions, 50–100 ms before the spike. This is indicated by the yellow colors that represent excitation. Thus, the neuron exhibited a transient response to stimuli presented in specific parts of visual space, which in this case is the neuron's current RF.

We can now use the same framework of reverse correlation to plot the RF of the same neuron around the time of a saccade (Figure 5D–F); again, yellow colors correspond to excitatory regions, and blue colors correspond to suppressive regions. Importantly, time 0 in these plots is now the time of saccade offset. The map shows the positions of stimuli most often associated with a spike fired at 100 ms after the saccade. Figure 5D and E shows cartoon plots of perisaccadic RFs expected from two predictions: first, for a scenario where there is no remapping (Figure 5D), there should be a yellowish blob of excitatory region at the current field corresponding to stimulus flashed 50–100 ms before the spike. The second prediction (Figure 5E) for the case of forward remapping is that there should be an excitatory region at the FF (top left) corresponding to stimulus flashed before the onset of the saccade. Figure 5F shows the empirical result for the same neuron as in 5C: there are now two spatial regions in which a stimulus can cause the neuron to fire. The first region corresponds to a stimulus flashed ~200 ms before the onset of the saccade and ~300 ms before the spike (yellow blob, top left). This spatial location corresponds to the FF. The second (yellow blob, bottom right) is a stimulus flashed 50–100 ms before the spike; this is the same current field as that observed during fixation (Figure 5C).

Although this might be considered a confusing way to plot the data, it emphasizes an important point: spiking activity in the immediate postsaccadic period combines information about presaccadic and postsaccadic stimuli. That is, the long latency of FF responses causes them to arrive in V4 at the same time as the postsaccadic visual response, so that neurons can integrate both views in the same spiking response (Burr and Morrone, 2011; Cicchini et al., 2013). For natural stimuli that do not change during

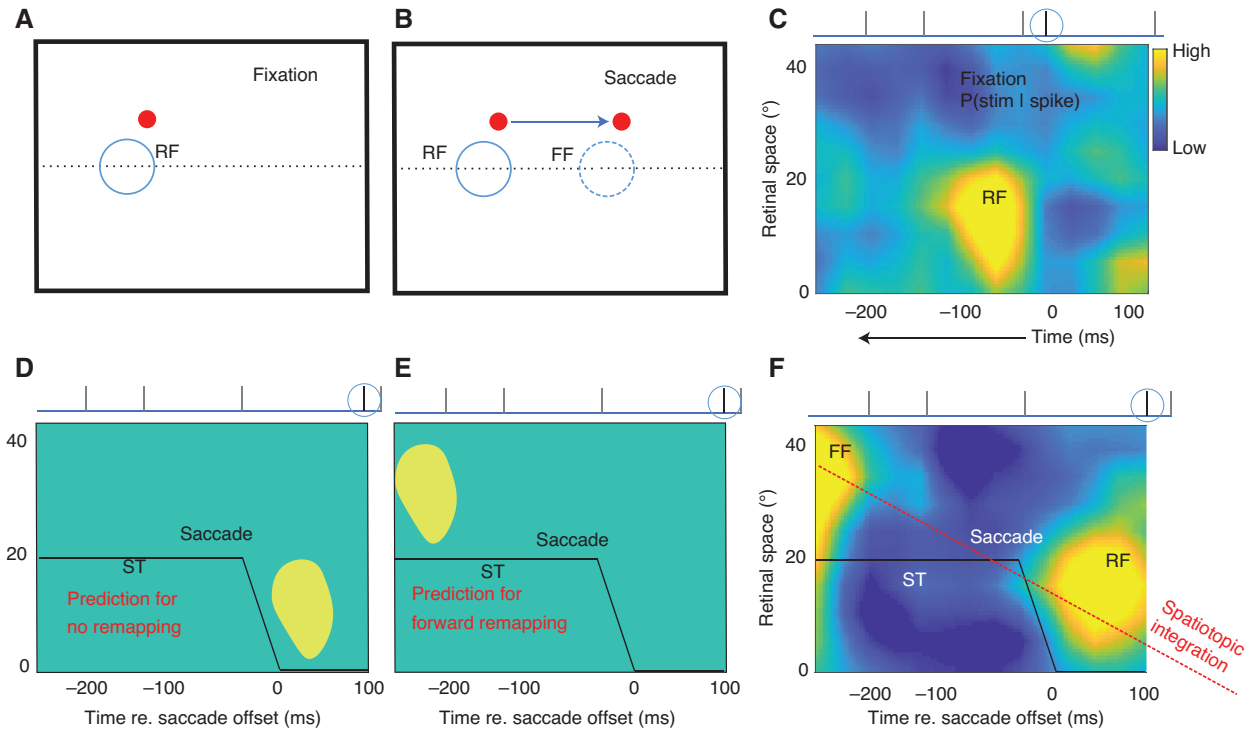

Figure 5: Reverse correlation approach to visualize the perisaccadic spatiotemporal RF.
(A and B) Location of RF and FF of a hypothetical neuron during fixation (A) and horizontal saccade (B). (C) Using reverse correlation approach, we demonstrate the average space-time pattern of stimuli that elicit a spike in a V4 neuron during fixation. (D and E) Using the same approach in the saccade condition, hypothetical plots for the V4 neuron in the case of no remapping (D) and when there is forward remapping (E). (F) Average space-time pattern of stimuli that elicit a spike in the same V4 neuron during the time of a saccade. Perisaccadic plot shows three distinct components corresponding to RF (yellow), FF (yellow), and a saccadic suppression component (blue). The remapped response to a presaccadic visual stimulus arrives at the same time as the afferent postsaccadic response. Thus, remapping could serve to integrate presaccadic and postsaccadic views of the same stimulus by bringing their neural responses into temporal alignment.

saccades, this mechanism is well suited to support the integration of visual information across saccades.

A number of psychophysical observations are consistent with this view. First, psychophysical observers do indeed integrate stimulus information across saccades, leading to better perception of orientation (Ganmor et al., 2015; Wolf and Schütz, 2015), shape (Harrison and Bex, 2014), motion (Szinte et al., 2016), color (Oostwoud Wijdenes et al., 2015), and natural images (Edwards et al., 2018). A typical finding is that a presaccadic view of a stimulus facilitates perception when the postsaccadic view of the stimulus is noisy.

At the same time, observers often have difficulty reporting the position and timing of a visual stimulus presented around the time of a saccade (Ross et al., 1997; Morrone et al., 2005). This also makes sense in the context of the space-time map shown in Figure 5D, as visual cortex activity after the saccade does not precisely reflect the retinal position or timing of the stimulus. Rather postsaccadic responses in V4 are consistent with stimuli presented at a range of spatiotemporal positions, and it has been argued that this aspect of remapping can account for a number of well-known distortions in perisaccadic perception (Cicchini et al., 2013). Note that some of these perceptual effects can also be explained with reference to convergent remapping (Zirnsak et al., 2014), and this remains an area of active investigation.

A final point of interest in Figure 5F is that the execution of the saccade leads to the appearance of strong suppression (blue blob), which is also localized in space and time. The spatial position corresponds roughly to that of the fixation RF, indicating that stimuli presented in the retinal RF before the saccade are actively suppressed. This is consistent with the phenomenon of saccadic suppression, which has been shown to reduce neural responses throughout the visual system around the time of a saccade (Thiele et al., 2002; Krekelberg et al., 2003; Berman and Wurtz, 2011; Zanos et al., 2016). The specificity of the effect in these data are consistent with the psychophysical observation that saccades reset visual perception (Paradiso et al., 2012) by actively eliminating presaccadic stimulus representations.

The suppressive component of the space-time map in Figure 5F might also explain the observation that remapping is not observed when multiple stimuli are presented simultaneously (Churan et al., 2011; Joiner et al., 2011; Zanos et al., 2016). When multiple stimuli are presented before the saccade, some will activate the suppressive mechanism, whereas others will activate the excitatory mechanism. If care is not taken to separate these stimuli in space and time, the resulting responses will likely cancel out, leaving only the postsaccadic visual response. This is what is typically observed in experiments that make use of dense RF mapping approaches (Joiner et al., 2011; Zanos et al., 2016). Note that this observation does not mean that remapping cannot be useful in natural vision: what is important is not the number of stimuli per se but rather the overall structure of the scene. A saccade that brings a large, stable stimulus into an RF with weak presaccadic stimulation will yield the optimal response from this kind of RF structure. Psychophysical results show that such stimuli are particularly salient perceptually (Deubel et al., 2010).

Future work in neurophysiology of remapping

In the last few decades, significant progress has been made in our understanding of the visuomotor brain mechanisms underlying perceptual visual stability. More recently, the phenomenon of remapping has been enriched with more refined knowledge about its nature. The future of this subfield of neuroscience will be to link the neural phenomenon with visual function and behavior.

As mentioned before, neurophysiological studies have thus far done little to elucidate a functional role for remapping. A fruitful future study would combine the transsaccadic integration paradigm from psychophysical studies (Herwig, 2015) with a behavioral readout (Yao et al., 2016a), so that the neurophysiological properties of RF shifts could be linked to psychophysical performance on a trial-by-trial basis. Better still would be a causal manipulation, such as electrical or optogenetic stimulation, which could alter or abolish remapping in the context of an ongoing behavioral task. A similar manipulation has been shown to impair performance in a double-step saccade task (Sommer and Wurtz, 2002, 2006), but given the complex and widespread changes in visual processing elicited by saccades, one might expect to discover an impressive array of effects on perception and behavior.

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