Attention shift and remapping across saccades

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Chapter 1

General introduction

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Visual information is the most important information for humans and many other primates. It plays a vital role in the survival and general daily life of primates. However, the brain's capability to process information is limited and it would be overwhelming if all of the visual information in the visual field is processed equally. Several selection mechanisms are used to optimize and prioritize visual information processing. Covert selective attention and foveation are two of the most important selection mechanisms. Covert selective attention enhances the salience of spatial location, objects, or features in the peripheral visual field. Foveation directs the fovea, the region with the highest resolution on the retina, towards the most important and behaviorally relevant objects. Saccades, a type of fast eye movement, are executed to foveate among different objects in the environment and scrutinize them with overt attention. Both covert selective attention and foveation are used to select and optimize the information to be processed by the limited neural resources while subjects are exploring the environment and/or performing visual guided actions. Understanding the relationship between the two selection mechanisms is an important area of research in neuroscience. In this introduction, I will first introduce saccades and covert visual spatial attention, as well as the relationship and the cooperation between the two. Afterwards, I will focus on the trans-saccadic information processing named remapping, introducing its properties, mechanisms, and possible functions.

1 Spatial attention and its relationship to saccade

1.1 Attention and its functions

"*Everyone knows what attention is. It is the taking possession by the mind in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought...It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state*."

–William James, 1890

This is how William James, one of the leading psychologists and philosophers in nineteenth century, labeled as the 'Father of American psychology', defined attention in his work 'Principles of Psychology'. He implied that attention was a process, which selects which information to be prioritized. Attention is important to our survival, because our information processing capacity is limited, and the amount of sensory information to be processed is huge, especially visual information. If we could not use attention to select the information that we need, we would be in a '*confused, dazed, scatterbrained state'* as James mentioned above ((James, 1890), page: 403). In daily life, we normally only focus our attention on one thing. Attention is classified into two types depending on whether the attended location and the gaze location overlap. If the attended location overlaps with the gaze location, it is called overt attention; if the attended location is in the peripheral visual field other than the gaze location, it is called covert attention. In addition, attention can be controlled by external or environmental stimuli, such as onset, flash, or sudden change of a stimulus; or, by internal states such as goals, rewards and tasks. These are called exogenous attention and endogenous attention respectively, or bottom-up and top-down attention (Posner, 1980). Bottom-up attention is attracted by the stimulus saliency, and is considered to be automatic and reflexive, it often induces a reflexive saccade (Friesen and Kingstone, 2003; Mayer, Dorflinger, Rao et al., 2004). In contrast, top-down attention is thought to be voluntary. Visual attention is also classified into spatial attention, object-based attention and feature-based attention. Spatial attention selects a specific region of the space to attend; everything including the objects and features in this region are attended, whereas object and feature-based attention select a single or a few objects and features to attend irrelevant of the spatial location (Posner, 1980; Tootell, Hadjikhani, Hall et al., 1998). In this thesis, I will focus on top-down, spatial covert attention, which is the best-studied type of attention.

Spatial attention has been likened to a spotlight (Posner, 1980) that enhances information processing in the brain at the attended location. The size of the attended location can be adjusted voluntarily, but the processing efficiency for given sub-location may decrease when the size of the attended location increases (Castiello and Umilta, 1990; Eriksen, Webb and Fournier, 1990). Previous studies have shown that directing attention to a region will improve performance if the task-relevant stimulus is in that region. Some studies showed that not only performance but also appearance is improved by attention (Carrasco, Ling and Read, 2004).

On the neuronal level, the modulation of spatial attention has been found in almost all visual and visuomotor areas in the brain by recording single neuron signals when the animals are trained to respond to a target. The target is either in the neuron's receptive field (RF), a special region of the visual space in which a visual stimulus will result in a response of that neuron, or out of the recorded neuron's RF in different trials. Frontal and parietal cortical areas such as frontal eye field (FEF) and lateral intraparietal area (LIP) have been reported to be particularly well involved in attentional modulation, some neurons in these areas not only showed higher response when there was a task relevant stimulus in their RF, some of them also controlled the attention enhancement in the lower brain areas (such as V1, MT, V4 etc.) (Goldberg, Bisley, Powell et al., 2006; Wardak, Olivier and Duhamel, 2011; Rao, DeAngelis and Snyder, 2012). In most cases (not always), the firing rate will be higher when the task relevant or target stimulus is located in the neuron's RF compare to when there is a task irrelevant or distracter stimulus in the neuron's RF (Moran and Desimone, 1985; Treue and Maunsell, 1996; Luck, Chelazzi, Hillyard et al., 1997). Attention not only modulates the neuronal firing rate(Petersen, Robinson and Morris, 1987; Treue and Martinez Trujillo, 1999; Ignashchenkova, Dicke, Haarmeier et al., 2004; Buschman and Miller, 2007; Buffalo, Fries, Landman et al., 2010; Rao, DeAngelis and Snyder, 2012); it also increases the gamma-band LFP (local field potential) power(Fries, Womelsdorf, Oostenveld et al., 2008; Gregoriou, Gotts, Zhou et al., 2009), local and cross-areal gamma-band coherence(Saalmann, Pigarev and Vidyasagar, 2007; Gregoriou, Gotts, Zhou et al., 2009), and decreases the neuronal response variability (fano factor) (Mitchell, Sundberg and Reynolds, 2007; Cohen and Maunsell, 2009), low frequency synchrony (Fries, Womelsdorf, Oostenveld et al., 2008) and correlated noise at low frequencies (Cohen and Maunsell, 2009). In addition, attention also modulates properties (such as size, shape, location of peak response etc.) of a neuron's RF ((Womelsdorf, Anton-Erxleben, Pieper et al., 2006; Anton-Erxleben, Stephan and Treue, 2009); for a review see (Noudoost, Chang, Steinmetz et al., 2010)).

1.2 Saccade

A saccade is a quick, simultaneous, coordinated movement of both eyes between two phases of fixation. Saccades bring objects or locations onto the foveal part of the retina, where the sharpest visual accuracy is found, to allow better analysis and processing of the

corresponding information. Saccades are the fastest eye movement and typically occur several times each second (Snodderly, 1987). Peak velocity is from tens up to 800 angular degrees per seconds and duration ranges from 10 to 100 ms depending on the amplitude of the saccade (Bahill, Bahill, Clark et al., 1975). This high velocity minimizes the time between two fixations and leaves more time to analyze visual information arising from stable fixation. Brain areas such as FEF, LIP, superior colliculus (SC) are highly involved in the preparation and control of saccadic eye movements. For example, some neurons in these brain areas change their responses before a saccade, and are tuned to different saccadic parameters such as saccade direction, amplitude, velocity etc. (Pierrot-Deseilligny, Rivaud, Gaymard et al., 1995; Gaymard, 2012).

1.2.1 Saccadic suppression

As mentioned above, saccades rapidly and frequently displace the images on the retina, which should produce a strong blur of the scene when natural viewing of the environment. However, we do not see such blur, instead we perceive a clear and stable world. The blurred images on the retina therefore seem to be suppressed, and this suppression of visual information processing is called saccadic suppression (Bridgeman, Hendry and Stark, 1975; Volkmann, 1986). Psychophysical studies have found saccadic suppression shortly before and during saccades, such as elevated detection thresholds for visual flashes (Zuber and Stark, 1966), motion changes (Burr, Holt, Johnstone et al., 1982), object displacement (Bridgeman, Hendry and Stark, 1975) etc. But saccadic suppression has been found to be absent or weak in some tasks, for example, detecting low spatial frequency patterns and in color discrimination tasks (Burr, Holt, Johnstone et al., 1982; Burr, Morrone and Ross, 1994; Diamond, Ross and Morrone, 2000), which suggests saccade suppression affect differently on different tasks that may relate to different pathways in the brain. In a discrimination task, Diamond and colleagues found that saccadic suppression started at about 50 ms before saccade onset and lasted for another 50 ms after saccade offset (Diamond, Ross and Morrone, 2000). Electrophysiological results also reported saccadic suppression in visual brain areas, such as LGN (lateral geniculate nucleus), V1, V2, V3, V4, MT (middle temporal), MST (medial superior temporal), pulvinar, SC etc. (Robinson and Wurtz, 1976; Reppas, Usrey and Reid, 2002; Thiele, Henning, Kubischik et al., 2002; Sylvester and Rees, 2006; Ibbotson, Price, Crowder et al., 2007; Kagan, Gur and Snodderly, 2008; Berman and Wurtz,

2011; Hass and Horwitz, 2011; Zanos, Mineault, Guitton et al., 2016). These visual areas are not found to participate in saccade control, however, the response are significantly suppressed by saccade.

The mechanisms underlying saccadic suppression are not yet well understood. Pre- and post-saccadic visual masking and corollary discharge/efference copy signal have been proposed to explain saccade suppression (Ross, Morrone, Goldberg et al., 2001; Wurtz, 2008; Wurtz, McAlonan, Cavanaugh et al., 2011). Visual masking normally means the perception of a visual target stimulus is impaired by the presence of a mask stimulus; the mask stimulus could be presented shortly before or after the target stimulus. The visual masking theory suggests saccadic suppression results from forward and backward masking effects of pre- and post-saccadic visual stimuli. Saccadic suppression is absent or weak when only the target stimulus is presented during a saccade and no other stimuli are displayed before and after saccade (Deubel, Elsner and Hauske, 1987; Castet and Masson, 2000; Castet, Jeanjean and Masson, 2002). Wurtz and colleagues suggest that a corollary discharge (CD)—an extra-retinal signal or an internal copy containing impending saccadic eye movement commands (Sperry, 1950; Matthews, 1982), plays an important role in saccadic suppression. An important piece of evidence supporting this theory is the observation that saccadic suppression precedes the onset of saccades (Wurtz, 2008; Wurtz, Joiner and Berman, 2011; Wurtz, McAlonan, Cavanaugh et al., 2011). An electrophysiological study in non-human primates also suggested that corollary discharge might contribute to the saccade suppression. When the eye muscles were paralyzed (the monkeys were unable to execute saccades), but the monkeys were trained to try making saccades, the background responses of neurons in V1 were suppressed (Judge, Wurtz and Richmond, 1980). However, in a behavioral experiment with human subjects viewing natural scenes, Dorr and Bex found that saccadic suppression could be explained by the high speed of the moving image on the retina caused by a saccade. They concluded that saccadic suppression during natural vision does not have to derive from an active extra-retinal mechanism but can result only from the blur caused by the fast eye movement (Dorr and Bex, 2013). However, the authors did not explain why saccade suppression could happen before saccade onset.

1.3 Relationship between spatial attention and saccades

Saccades bring relevant and important objects or locations to the fovea from peripheral visual locations to facilitate their processing; attention selects which information should be processed and guides saccade. The relationship between attention and saccades is mutually beneficial when the saccade and attention target overlap. It is possible that saccade target selection and attention target selection share the same neural mechanisms. Previous studies have provided abundant evidence for overlapped neural mechanisms that control saccade and spatial attention (Kowler, 2011). For example, previous studies have revealed that brain areas FEF, LIP and SC are highly involved in both attention modulation and saccade control. Some psychophysical evidence has demonstrated the impact of covert orienting of visual spatial attention on saccades. For example, there are studies showing that deviation of saccade trajectories depends on the attended location (Rizzolatti, Riggio, Dascola et al., 1987). A similar psychophysical study also demonstrated that covert spatial attention perturbed saccade preparation or programming (Kowler, Anderson, Dosher et al., 1995).

Saccade preparation has also been reported to show influence on attention and on subjects' performance. For example, in a study, the subjects were asked to make a saccade to a peripheral location while detect a visual stimulus presented before the saccade, the authors found that detection accuracy was highest when the visual target was located at the same location as the saccade target. In addition, when the visual target and saccade target were mismatched (i.e. not at the same location), detection accuracy was impaired compared to the detection-only task (without a saccade). The authors suggested that spatial attention was involved in saccade programming and/or execution (Hoffman and Subramaniam, 1995). Similar results were reported in other psychophysical studies (Deubel and Schneider, 1996; Deubel, 2008). On the neuronal level, several studies have shown that when there was a saccade target in the neuron's RF, the neuron's response was enhanced before saccade as if saccade targets attracted attention automatically, which suggests an influence of saccade preparation on attention (Gottlieb, Kusunoki and Goldberg, 1998; Moore, Tolias and Schiller, 1998; Steinmetz and Moore, 2014). Micro-electrical or TMS stimulation of oculomotor areas such as FEF and SC improved animal and human subjects' performance (Grosbras and Paus, 2002; Cavanaugh and Wurtz, 2004; Moore and Fallah, 2004; Chambers and Mattingley, 2005; Muller, Philiastides and

Newsome, 2005) as well as modulated the response of lower visual hierarchical areas (Moore and Armstrong, 2003). These results support the 'premotor theory of attention', which proposes shared neuronal mechanisms for saccade preparation/programming and covert spatial attention (Rizzolatti, Riggio, Dascola et al., 1987; Corbetta, 1998; Corbetta, Akbudak, Conturo et al., 1998).

But other studies have argued against the 'premotor theory' (Morgan, Ball and Smith, 2014). It is possible that these two systems are parallel but distinct; they just act in a similar way. Some physiological studies performed in monkeys have investigated the relationship between the two systems by perturbing neural signals in one system while examining the other at the same time. For example, by using micro-stimulation in SC or FEF, and simultaneously recording from neurons in other visual areas like MT or V4, it is possible to address the causal relationships of neural signals between the oculomotor system and spatial attention system. Some studies have confirmed that different functional roles were played by distinct neuronal subgroups in FEF, SC and LIP (Ignashchenkova, Dicke, Haarmeier et al., 2004; Thompson, Biscoe and Sato, 2005; Brown, Hanes, Schall et al., 2008). Visual neurons, visuomotor neurons and motor neurons are coexistent in brain areas of LIP, SC and FEF. Visual neurons respond only to the visual stimuli presented in their RF; motor neurons respond only to eye movements or/and limb movements to the neuron's response field; visuomotor neurons respond to both visual stimuli and eye/limb movements. Thompson and colleagues found that when monkeys were doing a covert attention task without eye movement, the responses of visual neurons and visuomotor neurons were enhanced, whereas the motor neurons were not enhanced, even showing inhibition in FEF (Thompson, Biscoe and Sato, 2005). A similar observation was reported by recording single neurons from SC when monkeys performed a covert spatial attention task. The results showed that only the visual and visuomotor neurons were enhanced by attention, but not motor neurons in SC (Ignashchenkova, Dicke, Haarmeier et al., 2004). Other studies also confirmed that different functional roles were played by distinct neuronal subgroups (Brown, Hanes, Schall et al., 2008). Moreover, inactivation of LIP did not impair saccade parameters but indeed impaired the animal's visual search task (Wardak, Olivier and Duhamel, 2002, 2004). The authors suggested that LIP 'is not involved in the saccadic execution *per se*', but is involved in processes such as salience representation (Wardak, Olivier and Duhamel, 2011).

The psychophysical studies and stimulation studies mentioned above suggest shared mechanisms behind covert spatial attention and saccade preparation. However, single neuron data and inactivation studies suggest a dissociation of the two. Visual neurons are more involved in selecting the visual target and motor neurons are more involved in saccade programming. More studies are needed in the future to better understand the mechanisms behind the two.

1.4 Shifting of spatial attention

In daily life, spatial attention typically overlaps with where we are looking, which means that attention modulates the neurons with foveal receptive fields. In this situation, spatial attention does not have to modulate different neurons in the brain; instead, we make saccades to select different targets when we view our environment. However, attention does not always modulate foveal neurons. There are at least two processes requiring attention shifts between different groups of neurons. One is when subjects are fixating at one location and shift attention among different objects in the peripheral visual field. For example, when we are driving towards an intersection, we shift attention from side to side while looking at the vehicles before ours. Attention has to shift from one group of neurons to another (the neurons with left RFs to neurons with right RFs for example). The other situation is when the target object is stable while our eyes, head and/or body is moving, which means the target images on the retina are changing, resulting in the need for an attention shift among neurons in the brain. In the following section, I will review the existing literature of attention shift studies related to these two situations.

1.4.1 Attention shift with fixation

It is possible and common that human and non-human primates covertly shift attention between different locations in the visual field while keeping the eyes at fixation. Several studies have investigated covert spatial attention shifts in visual areas such as LIP and MT. In a study recording from MT neurons, Busse and colleagues (2008) used a double-cueing paradigm. The monkeys were trained to covertly attend to one target random dot pattern (RDP) out of three RDPs, indicated by the first exogenous cue. In one experimental condition, the monkeys had to endogenously/voluntarily covertly shift their spatial attention to another of the three RDPs, indicated by the second cue. By manipulating the

combination of the first and second cued RDP locations, spatial attention could shift into or out of the recorded neuron's RF. The results suggested that the exogenous attention induced by the onset of the cue took about 120 ms to affect the MT neuron's response. The latency of endogenous attention shifting into the neuron's RF was about 190 ms after the second cue onset. Finally, the authors found that the disengagement time of spatial attention from the recorded neuron's RF was about 300ms after the cue shifting the monkey's attention out of the neuron's RF (Busse, Katzner and Treue, 2008).

Herrington and Assad used a similar paradigm to investigate the temporal dynamics of covert attention shifts in LIP and MT. They found that LIP neurons were significantly enhanced earlier than MT neurons after cue onset when the attention was shifted into the neuron's RF. It took about 200ms (median: 166ms for one monkey, 230ms for another) in LIP and 250ms in MT (median: 228ms for one monkey, 280ms for another). Similar to the above study, they found that attention also took longer (305ms in LIP; 348ms in MT) to fade away when attention was shifted out of the neuron's RF compared with the speed of attention engagement in both brain areas (Herrington and Assad, 2009, 2010).

These studies, along with a study recording neurons in V1 (Khayat, Spekreijse and Roelfsema, 2004), suggest that when the animals are trained to shift attention while maintaining eye fixation, the engagement of attention modulation takes more than 100 ms after cue onset, and it is faster than disengagement in visual areas. In addition, the studies confirm that covert attention shifts are a top-down process initiating from parietal or frontal areas and then transfering to lower visual areas like MT. The studies also support the theory that the origin of attention is in parietal or frontal cortex.

Previous studies suggest that it takes about one hundred milliseconds to several hundred milliseconds to covertly shift attention modulation from one neuron to the other when the eyes maintain fixation. However, attention shifts across saccades among neurons seems to use a different mechanism to covert attention shifts. Some studies suggested that the attention modulation might shift to other neurons before a saccade in the form of 'attention pointers' (Cavanagh, Hunt, Afraz et al., 2010c). We will discuss this issue in the later part.

1.4.2 Attention shift across saccade

The other situation in which spatial attention benefit has to shift across neurons in retinotopic visual areas is when the target object is stable and the subject is making eye or head movements. In this case, the target will be transferred across saccades from RFs of one group of neurons to another. Because spatial attention only benefits neurons whose RFs cover the target, spatial attention benefit transfers from the neurons whose RFs cover the target before the saccade to the neurons with RFs covering the target after the saccade. Therefore, in retinotopic areas, attention modulation has to be reestablished in one group of neurons, and fade away from another group.

In a physiological study, Khayat and colleagues investigated the reestablishment of object-based attention modulation after a saccade. Two curves were displayed on the screen after a short fixation. The monkeys were required to make two saccades along the target curve and ignore the distractor one. Multi-unit activity in V1 was recorded while the monkeys were doing the task. In one condition, part of the target curve was brought into the RF of the multi-units by the first saccade. The results showed that the attentional enhancement was reestablished rapidly after the first saccade. It is about 50 ms faster than when the target curve was directly displayed in the RF of the multi-units. The authors suggested that the results might indicate remapping of attention (Khayat, Spekreijse and Roelfsema, 2004). However, pre-saccadic remapping was not found in V1. The authors suggested that the attention enhancement in V1 might have been gated by the visual stimulus (Khayat, Spekreijse and Roelfsema, 2004). Because there was no stimulus in the units' RF before the first saccade, it is impossible to quantify the attention enhancement if the attentional modulation arrived in V1 before the first saccade. Moreover, they did not investigate the time course of how attention faded away after a saccade when the target was brought out of the neuron's RF. Whether object-based attention and spatial attention share the same neuronal mechanisms remains unknown. In this thesis, we use a spatial attention paradigm; and try to demonstrate the complete dynamics of attention shifts across saccade in visual area MT.

Attention shifts across saccades is highly related to a phenomenon called trans-saccadic remapping (Cavanagh, Hunt, Afraz et al., 2010). In the following sections of this introduction, I will review the related psychophysical studies on human and neuronal physiological studies on non-human primates.

2. Remapping across saccades

2.1 Remapping

The visual and visuomotor areas are organized in a retinotopic pattern; the adjacent neurons in these brain areas have slightly different RFs. These RFs form an orderly and systematically map covering the visual field. Because of this organized arrangement of the neurons' RFs, the neurons in these areas could be seen as formatting a whole map of the visual field. Each visual neuron in these areas has a RF corresponding to a region on the retina, and the neuron only responds to the stimulus located inside its RF. When the eyes are moving, the RF of a specific neuron therefore corresponds to different spatial locations in the environment, directly dependent on the current location of the eyes. However, some neurons in visual or visuomotor areas, such as LIP, FEF, SC, also respond to a flashed visual stimulus at the location that an upcoming saccade will bring into the RF. Importantly, the stimulus is not in the neuron's classical retinotopic RF before or after saccade, it only flashes briefly before saccade onset in the neurons' post-saccadic RFs. It seems therefore that these neurons either predict the occurrence of a stimulus will be brought into the RF by the upcoming saccade, or they remember there was a stimulus appearing before the last saccde in the post-saccadic RF location. This peri-saccadic neuronal activity, which the neurons will change their responses before or after saccade when a stimulus flashed in the post-saccadic RF, is called remapping. It has been proposed as an important mechanism for visual stability and keeping track of objects across saccades (Wurtz, 2008; Burr and Morrone, 2011; Hall and Colby, 2011; Mathot and Theeuwes, 2011; Melcher, 2011; Wurtz, Joiner and Berman, 2011; Mirpour and Bisley, 2012; Higgins and Rayner, 2015; Rolfs, 2015; Marino and Mazer, 2016). Two types of remapping are distinguished regarding the temporal dynamics of the activity: 1) predictive remapping, and 2) post-saccadic memory traces. In the first case, when a stimulus was brought into a neuron's RF, this neuron will change its response *before* the saccade is executed, or the latency of the evoked response is shorter than the normal visual response when a stimulus appears in the neuron's RF. On the other hand, when the evoked response occurs only *after* the saccade, and has longer latency than the normal visual response, this response is referred as post-saccadic remapping.

However, the research results regarding the spatial dynamics (i.e., receptive field dynamics) of remapping responses are inconsistent (Melcher, 2011). Some studies suggest a jump of

the RF from the pre-saccadic RF to post-saccadic RF (Wurtz, Joiner and Berman, 2011); some suggest that the RF shifts towards the saccade target (Zirnsak and Moore, 2014; Zirnsak, Steinmetz, Noudoost et al., 2014); some suggest both of the above shifts (Neupane, Guitton and Pack, 2016); and some suggest expansion of the RF (Wang, Fung, Guan et al., 2016). Therefore, the exact spatial properties of remapping require more investigation.

2.1.1 Physiological studies

The first descriptions of remapping in single-neuron recording studies were reported in FEF (Goldberg and Bruce, 1990) and LIP (Barash, Bracewell, Fogassi et al., 1991) using the double-step paradigm. This paradigm requires the monkeys to make two successive saccades to two saccade target locations that are briefly presented before the first saccade. The disappearance of the saccade targets signals the movement of the eyes. In this paradigm, the subjects have to prepare both of the upcoming saccades before the first saccade. The authors found that if the second saccade target was brought into the recorded neuron's RF by the first saccade, neurons showed higher responses, even though the saccade targets were removed before the eyes moved, and no visual stimulus was present in the neuron's RF before and after saccade. This was explained as the remapping of the second saccade target, i.e. the neuron responded to the remapped memory trace of the second saccade target (Mathot and Theeuwes, 2011).

In a landmark remapping study (Duhamel, Colby and Goldberg, 1992), the authors recorded neuronal responses in LIP while the trained monkeys made saccades to a saccade target. In one condition, a visual stimulus was presented in the neuron's post-saccadic RF, and no stimulus was presented in the neuron's pre-saccadic RF. They found some LIP neurons had a higher response just before saccade, which was proposed as predictive remapping. In another condition, the visual stimulus was only briefly flashed in the neuron's post-saccadic RF before saccade; thus, there was no stimulus in the neuron's RF before and after saccade. However, some neurons still had a higher response after saccade compared with the simple saccade condition, as if the neurons remembered there was a stimulus in the post-saccadic RF location. The authors proposed this response to reflect the other remapping activity, namely a memory trace (Figure 1). This remapping activity is not a pure visual response, because the neurons do not respond to the stimulus in the post-saccadic RF unless a saccade is made. It is also not a motor response, because the neurons do not show remapping activity when a simple saccade is made. Rather, the remapping

activity reflects the neurons' expectation that the visual stimulus will be brought into their RF by a saccade (predictive remapping); or, the neurons are 'remembering' that the visual stimulus is in their post-saccadic RF (post-saccadic memory trace). Further properties (spatial and temporal) of remapping activity in LIP were revealed by later studies (Colby, Duhamel and Goldberg, 1996; Kusunoki and Goldberg, 2003; Heiser and Colby, 2006).

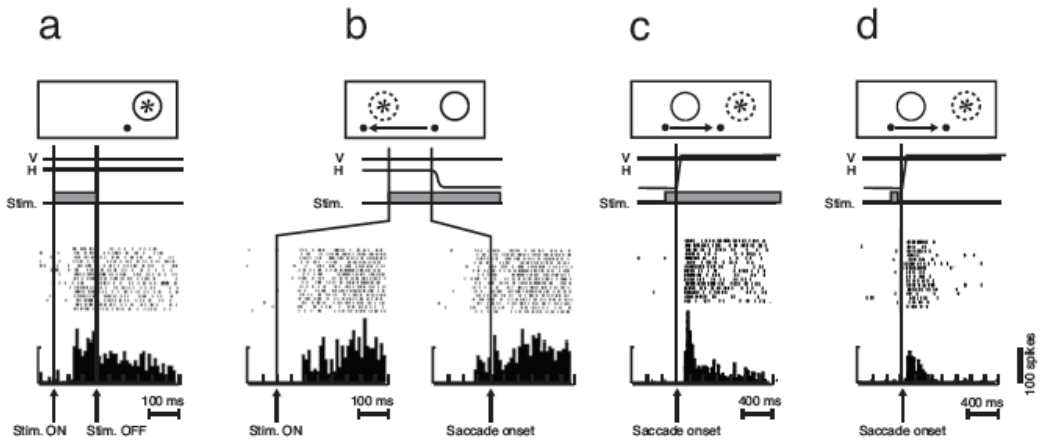

Figure 1. Neuronal remapping in LIP. Top row rectangles show the paradigm used in each condition of the experiment. Dots, star, circle, dashed circle, and arrow indicate the fixation and saccade targets, visual stimulus, pre-saccade RF, post-saccade RF, saccade, respectively. The time lines below the rectangles show the vertical (V) and horizontal (H) eye position, as well as the times in which the visual stimulus was displayed (Stim.). The raster plots show example neurons responses to each condition, each row indicates one trial. Spike density histograms are shown below. The histograms and the raster plots are aligned to the vertical lines indicating events within a trial. The time scales below the histograms indicate 100 ms (a, b) or 400 ms (c, d). **(a)** The example neuron responds to the visual stimulus presented within the RF in a fixation task. The neuron shows a normal visual response. **(b)** The neuron responds to the visual stimulus that is brought into its RF by a saccade. Data are aligned to stimulus onset in the left panel and to the saccade onset in the right panel. This neuron shows a pre-saccadic predictive remapping response. **(c)** Another example neuron that do not show a pre-saccadic predictive remapping – the neuron shows no response until after the saccade is made. **(d)** The same neuron as (c) discharges when a saccade brings a pre-saccadically flashed visual stimulus into its RF after saccade, even though the stimulus is never present in its RF. This neuron shows a remapped memory trace. (Adapted from Duhamel, Colby and Goldberg, 1992)

Remapping activity has also been found in other brain areas such as frontal eye field (FEF) (Umeno and Goldberg, 1997, 2001; Sommer and Wurtz, 2004, 2006, 2008), superior colliculus (SC) (Walker, Fitzgibbon and Goldberg, 1995; Dunn, Hall and Colby, 2010; Churan, Guitton and Pack, 2012) medial superior temporal area (MST) (Inaba and Kawano, 2014)and in the ventral stream in areas V4, V3a, V3 and V2 (Tolias, Moore, Smirnakis et al., 2001; Nakamura and Colby, 2002; Neupane, Guitton and Pack, 2016) using similar paradigms. Remapping activity is not identical in different brain areas, though it has been found in the brain areas mentioned above. The variety of the remapping activity reported in these studies showed some trends along the visual hierarchy. First, the proportion of neurons showing remapping activity decreases when moving down the visual hierarchy. For example, nearly all neurons (96%) in LIP show remapping activity (Duhamel, Colby and Goldberg, 1992), about half (52%) in V3A, and the proportion drops to 35% in V3, 11% in V2 and 2% in V1 (Nakamura and Colby, 2002). Predictive remapping shows a similar tendency, it was reported in around 44% of LIP neurons (Duhamel, Colby and Goldberg, 1992) and decreases to 35% in V3A (Nakamura and Colby, 2002). No predictive remapping was found in MT, V2 or V1 (Nakamura and Colby, 2002; Ong and Bisley, 2011). Second, the strength of remapping activity also decreases down the visual hierarchy (Gottlieb, 2007; Merriam, Genovese and Colby, 2007). Third, the mean latency of neuronal remapping activity relative to saccade onset showed an increase at lower levels of visual hierarchy (Nakamura and Colby, 2002; Higgins and Rayner, 2015).

Remapping is a clear and replicable phenomenon in many brain areas of non-human primates. Given that the detection of remapping requires relatively high spatial (the level of receptive fields) and temporal (ms) resolution, it is challenging to detect remapping in the human brain. Several brain imaging studies in human subjects have reported remapping responses in human brain using non-invasive techniques such as fMRI, magnetoencephalography (MEG) and electroencephalography (EEG). The rationale behind the experimental design is similar to the animal experiment. The stimulus was removed before saccade and transferred from one visual hemifield to the other, and therefore from one brain hemisphere to another, by a saccade. If the condition evoked a different response in the hemisphere ipsilateral to the hemifield of initial stimulus presentation compared to control (pure motor or visual response), it was judged as evidence for remapping.

For example, in an fMRI study, a visual stimulus was presented in one visual field (left hemifield for example) only before saccade, and the subjects were asked to make a left saccade beyond the stimulus. The stimulus would then be located in the right visual hemifield after the saccade. If the task evoked a change in BOLD (blood-oxygenation level dependent) signal of the left hemisphere after saccade compared to control conditions, it is interpreted as a remapping signal because there was no stimulus present in the corresponding visual field (right in this case) at any time across the trial. The authors indeed found such remapping BOLD signals in parietal cortex (Merriam, Genovese and Colby, 2003), in line with the results from the monkey electrophysiology experiments described above. Medendorp and colleagues also found BOLD and gamma-band (in MEG signal) remapping signal in parietal cortex using a double-step task (Medendorp, Goltz, Vilis et al., 2003; Medendorp, Goltz and Vilis, 2006; Van Der Werf, Jensen, Fries et al., 2008). Similar remapping signals were found in visual cortex from V1 to V4 using a similar paradigm (Merriam, Genovese and Colby, 2007). The results also suggested that the strength of remapping decreases along the visual hierarchy from high to low areas, which is consistent with electrophysiological data from monkeys (Nakamura and Colby, 2002; Merriam, Genovese and Colby, 2007). MT has also been reported to show remapping in an fMRI experiment (d'Avossa, Tosetti, Crespi et al., 2007). However, the low temporal resolution of fMRI makes it difficult to find a predictive remapping signal. EEG has been used to investigate predictive remapping in humans using similar experimental design to the studies mentioned above because of its higher temporal resolution. However, most studies failed to find any predictive remapping signal (Bellebaum, Hoffmann and Daum, 2005; Bellebaum and Daum, 2006; Parks and Corballis, 2008; Peterburs, Gajda, Hoffmann et al., 2011). The exception was one EEG study that found signal enhancement before saccade onset in some electrodes above the parietal cortex (Parks and Corballis, 2010).

2.1.2 Psychophysical studies

As demonstrated above, the strongest evidence for remapping has been found in experiments using extracellular recording in monkey brain. Psychophysical studies have also been performed to investigate the behavioral consequences of remapping in human subjects. Most of these studies used adaptation paradigms such as the tilt after-effect (TAE), motion after-effect (MAE), or face emotion adaptation. The logic underlying these experiments is that adaptation effects are often strongest when adaptor and test stimuli

are presented at the same retinotopic location (Dickinson, Mighall, Almeida et al., 2012). If remapping transfers feature information across a saccade, then an adaptation effect should be detectable at the remapped location. For example, in one study (Melcher, 2007) the subjects were asked to distinguish the tilt of a test grating (test) after adaptation by an adapting grating (adaptor) while preparing a saccade. In the important conditions, the adaptor was placed at the pre-saccadic initial fixation point (foveal region), and the test was presented either at the same location as the adaptor (the initial fixation point, i.e. the same spatiotopic location) or the location of the saccade target (i.e. the same retinotopic location). The test could be shown before or after saccade (Figure 2). The results showed that the TAE gradually increased before saccade onset when the test was placed at the saccade target location; at the same time, the TAE gradually decreased before saccade onset when the test was presented at the adaptor location (initial fixation location) even through the adaptor and the test were at the same retinotopic locantion. Together with other TAE studies (Melcher, 2005, 2009; Zimmermann, Morrone, Fink et al., 2013), the results suggested a transfer of the feature information just before saccade. Besides, in another experiment of the same study (Melcher, 2007), when the adaptor was shown at the initial fixation location, and the test was placed at an intermediate position between the initial fixation point and saccade target, human subjects also display a TAE before the saccade, which suggested remapping towards the saccade target or an expansion of neurons' RFs across saccade as mentioned in the physiological studies. MAE was also reported at the same spatiotopic location across saccades using a similar paradigm (Ezzati, Golzar and Afraz, 2008; Biber and Ilg, 2011; Turi and Burr, 2012; Yoshimoto, Uchida-Ota and Takeuchi, 2014). As well as TAE and MAE, Melcher also reported spatiotopic aftereffects for face, tilt and shape adaptation (Melcher, 2005). A face emotion after-effect after emotional adaptation at the same spatiotopic location after saccade has also been reported (Wolfe and Whitney, 2015).

However, the overall results of these psychophysical studies were inconsistent, and sometimes even contradictory. Some studies found the TAE only at the same retinotopic location but not the same spatiotopic location across saccades (Mathot and Theeuwes, 2010, 2013). Similarly inconsistent results were also reported for the MAE (Knapen, Rolfs and Cavanagh, 2009; Turi and Burr, 2012), face aftereffect (Afraz and Cavanagh, 2008), and direction aftereffect (Wenderoth and Wiese, 2008).

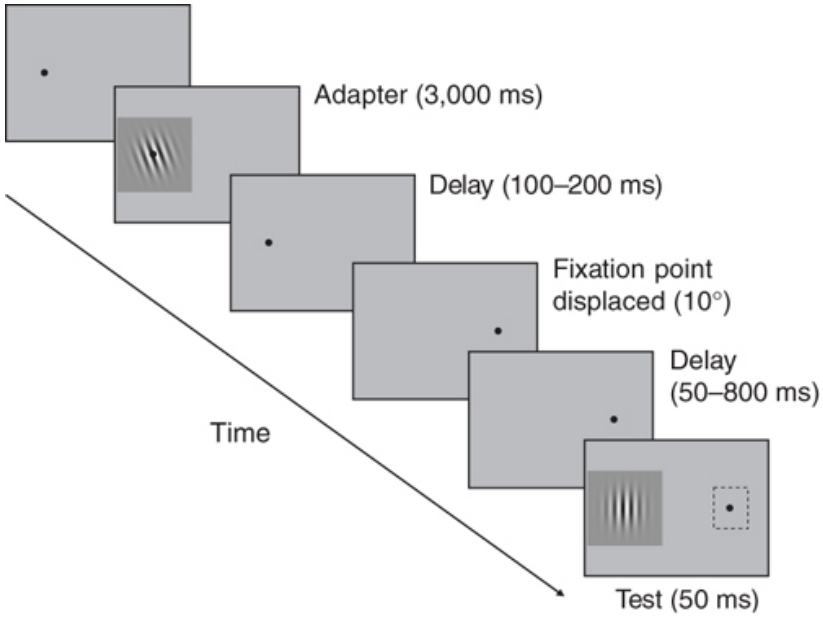

Figure 2. The paradigm of a TAE experiment. The grating indicates the visual stimuli, the dots indicates the fixation point and saccade target. After a short fixation, an adapter stimulus is shown at the fixation point for 3,000 ms. After a short delay, the fixation point jumps 10 degrees to the other side of the screen, which cues the subjects make a saccade to the new location. A test stimulus is shown for 50 ms after 50-800 ms of fixation point jumping, which allows the test could be shown before or after the saccade, the test stimulus is displayed either at the pre-saccadic fixation point (as the figure shows) or location of the post-saccadic fixation point (dashed square). (Adapted from Melcher, 2007)

For example, Afraz and Cavanagh only found retinotopic face aftereffects but not spatiotopic (Afraz and Cavanagh, 2008); and Mathot and Theeuwes reported the TAE was found only when the adaptor and the test were at the same retinotopic location, but not when the adaptor and the test shared the same spatiotopic location across saccade (Mathot and Theeuwes, 2013). Given these negative results on the spatiatopic aftereffect, Cavanagh and colleagues suggested that feature properties were not remapped across saccades; they suggested that remapping referred instead to a transfer of the attentional pointer in retinotopic brain areas (Cavanagh, Hunt, Afraz et al., 2010c; Cavanagh, Hunt, Afraz et al., 2010a). Others argued that the apparent spatiotopic integration of motion information across the saccade resulted noise in the perceptual system regarding the time of the

motion stimulus onset related to the saccade, and claimed that it might not have any practical function (Morris, Liu, Cropper et al., 2010).

On closer examination, there are some factors that might explain part of the variability in the psychophysical studies, for example, the differences in experimental method or/and stimuli used in the experiments. It seems that drifting Gabors and gratings were less likely (Wenderoth and Wiese, 2008) than random dot patterns (RDP) to elicit the MAE at spatiotopic locations (Ezzati, Golzar and Afraz, 2008; Wenderoth and Wiese, 2008; Knapen, Rolfs and Cavanagh, 2009; Turi and Burr, 2012). How the aftereffect was quantified might also be of importance. In different studies, different baseline and control conditions were used, which might result in inconsistencies (Marino and Mazer, 2016). Finally, the different duration between the test stimulus and saccade onset might contribute to the difference of the results (Turi and Burr, 2012).

In sum, based on current evidence it is unclear whether or not remapping transfers feature information across a saccade (spatiotopic aftereffect) in humans and in which cortical areas such a transfer might occur. For future studies, experimental methods, stimulus type, baseline conditions, and stimulus presentation timing should be well controlled to allow better comparison of the results of remapping in human subjects.

2.2 Corollary Discharge and remapping

Although remapping activity has been found in many areas of nan-human primate cortex, the underlying neural mechanisms and circuits are not well understood. Wurtz and colleges (Sommer and Wurtz, 2002, 2006, 2008; Wurtz, 2008; Wurtz, Joiner and Berman, 2011) proposed that the corollary discharge (CD, or efference copy), an internal copy containing impending saccadic eye movement commands (Sperry, 1950; Matthews, 1982), might contribute to remapping activity. SC was suggested as an ideal source of the CD because of the retinotopic map it contains and the direct control of eye movement. The CD originating from SC would likely contain information about the direction, amplitude, and velocity of the planned eye movement, and could be transfered to the cortex and act as remapping activity. Furthermore, they proposed the medial dorsal (MD) nucleus of the thalamus, an oculomotor area between motor area SC and visuomotor area FEF, as an important relay to transfer the CD from SC to cortex. In the seminal study of Sommer and Wurtz (2002), MD neurons were recorded when the monkeys were making simple

saccades. The results showed that the MD neurons responded before saccade onset, while inactivation of the MD did not change the saccade vector in speed, direction or amplitude. Both findings were consistent with CD signal. In a further condition, the monkeys were trained to perform a double-step saccade towards saccade targets that were removed before the first saccade onset. The disappearance of the saccade target before saccade onset forced the brain to take into account the vector of the first saccade to perform the second saccade correctly. The results of this condition showed that after inactivation of one side of the MD nucleus, the second saccade was impaired when the saccade targets were located in the contralateral visual field, which meant that the brain failed to take into account the vector of the first saccade (lost the CD signal) when preparing the second one. These results support a role of MD in relaying the CD signal.

In a subsequent study (Sommer and Wurtz, 2006), FEF neurons were recorded while the trained monkeys made a saccade, and a probe was flashed around the time of saccade either in the neuron's pre-saccadic or post-saccadic RF. Both predictive remapping and a memory trace were found in FEF. The authors also found that the visual responses of some neurons in FEF to the probe became weaker when it was flashed in the pre-saccadic RF just before a saccade, while the responses (remapping activity) became stronger when the probe was flashed in the post-saccadic RF at the same time. However, when the probe was flashed at the midpoint between pre-saccadic RF and post-saccadic RF, the neuron was unresponsive. This result suggested that the neuron's RF shifted rather than spanned the space to the post-saccade RF, which is in line with the predictions of the CD. More importantly, the authors found that the remapping activity in FEF was impaired after inactivation of MD by injection of muscimol, a selective agonist of GABA receptors. The authors thus suggested that the CD from the SC-MD-FEF pathway was necessary and sufficient to induce RF shifting (remapping) in FEF neurons. This demonstration provided a potential circuit-level explanation of how the corollary discharge originating from SC is transferred to cortex, and emerges as remapping.

The above findings provided a possible neuronal mechanism for remapping, and showed that MD inactivation impaired both the remapping response in FEF and the motor planning of the saccade in a double-step task. However, whether the SC-MD-FEF circuit directly affects the monkey's visual perception is not clear. If MD indeed relays the CD signal from SC to frontal cortex, inactivation of MD may impair the visual perception of the subject's

own saccade vector, but the saccade itself should be not influenced. This was found in a recent study (Cavanaugh, Berman, Joiner et al., 2016). The monkeys were trained to make a saccade to a target located on the left or right of fixation, but the target may jump a small distance (less than two degrees back or forth) during the execution of the saccade. The monkeys had to report the direction of the target displacement by moving a bar after saccade. The perception of the saccade end point (the report of the target displacement) and the actual saccade end point were decoupled by this paradigm. The authors found that, during unilateral MD inactivation with muscimol injection, the perception of the saccade towards the contralateral side was impaired, but the saccade itself was not affected as predicted. The authors therefor concluded that the CD signal containing internal information contributed to the perceived visual stability created by the brain. An earlier case study of a human patient with MD lesions reported a similar impairment in a double-step experimental paradigm, which strongly suggests that humans share the same CD circuit and function with monkeys (Bellebaum, Daum, Koch et al., 2005). These results suggest that the remapping CD not only affects neuronal responses, but also the subject's perception.

2.3 The role of attention in remapping

It is well known that attention modulates visual perception (Posner, 1980; Luck and Ford, 1998; Boynton, 2005). Previous studies also showed the influence of attention on remapping (for a review see Mathot and Theeuwes, 2011). In a classic study, Gottlieb and colleagues (1998) found that when a saccade brought a recently onset salient stimulus which was expected to capture exogenous/bottom-up attention into an LIP neuron's RF, the neuron showed higher remapping activity than when a stable stimulus which was presented on the screen for a long time, was brought into the neuron's receptive field. The recorded LIP neurons also showed similarly higher remapping activity when a task-relevant stimulus (a saccade target in this study) was brought into the RF by a saccade (Gottlieb, Kusunoki and Goldberg, 1998) (Figure 3). The results underline the importance of attention in remapping activity.

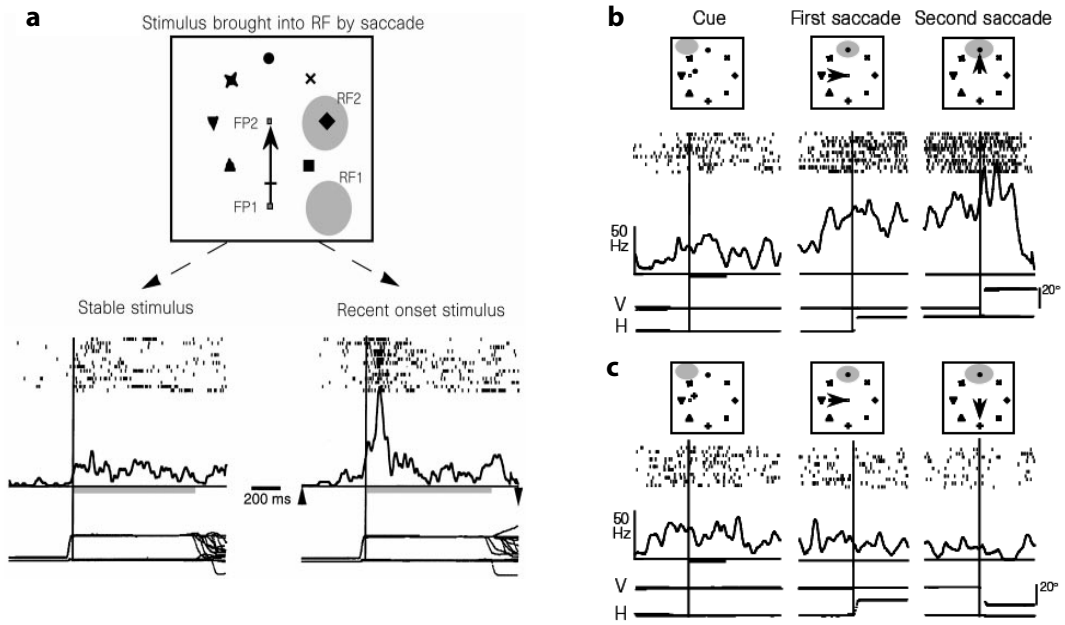

Figure 3. Example neurons respond to stable and recent onset stimulus (a), and stable saccade target (b) or distracter (c). The contents in the first row show the illustration of the visual display used by each condition in the experiment. The FP1, FP2, RF1, RF2, arrow represent the fixation point, saccade target, pre-saccadic RF, post-saccadic RF, saccade respectively. The eight components arranged in a circular are visual stimulus. Below the paradigm illustration, the raster plots and spike density histograms are shown. The time lines below the histograms show the vertical (V) and horizontal (H) eye position. The long vertical lines indicate the saccade offset (a), cue onset (b, c left panel), first saccade onset (b, c middle panel), and second onset (b, c right panel). **(a)** Neuron responses to a stable stimulus (left panel) or recent onset stimulus (right panel) that was brought into the RF by a saccade. The neuron has a stronger response when a recent onset stimulus was brought into the RF by saccade than when the stimulus was stable. **(b)** Neuron responses when a saccade target is brought into the neuron's RF by the first saccade while the monkeys are trained to make a two-step saccade to a cued stimulus. **(c)** Neuron responses when a non-saccade-target stimulus is brought into the neuron's RF. The neuron responded before the first saccade and lasted sometime after the second saccade when the RF stimulus was cued (b), but not responded when the opposite stimulus was cued (c). (Adapted from Gottlieb, Kusunoki and Goldberg, 1998)

The visual salience of a stimulus was also found to affect the remapping response in FEF (Joiner, Cavanaugh and Wurtz, 2011). In the study, when a visual stimulus which was presented in the post-saccadic RF of the recorded FEF neuron, was displayed together with distracters that were located outside of the post-saccadic RF, the remapping response was

significantly lower than when only the stimulus in the post-saccadic RF was presented. Because the distracters decreased the visual saliency of the stimulus in the post-saccadic RF, the stimulus in the post-saccadic RF attracted less bottom-up attention, which decreased the remapping response (Joiner, Cavanaugh and Wurtz, 2011). Together, these results suggest that the remapping response in LIP and FEF are modulated by saliency and attention. It is possible that only salient stimuli are remapped across saccades. However, as far as we know, no study has investigated effect of top-down attention on remapping. In this thesis, we designed a paradigm to investigate how the task related top-down attention affect the remapping response in MT neurons.

In a human psychophysical remapping study, an increased TAE was reported when subjects directed attention to the adapter stimulus (Melcher, 2009). Golomb and colleagues (2008) investigated spatial attention influences both retinotopically and spatiotopocally after saccade. They used a paradigm that probed spatial attention by a spatial cue at various times after saccades. The task required subjects to discriminate the orientation (left or right) of a target tilted bar. The target bar could be at different locations depending on the spatial cue (same retinotopic location, same spatiotopic location and control location). They found facilitation at the retinotopic location of the cue (i.e. when the target was at the same retinotopic location as the cue) for about 100-200 ms after saccade when the subjects were required to maintain attention at the spatiotopic location. This facilitation of the retinotopic representation was significant immediately after the saccade, although the retinotopic location was not task-relevant in this condition. However, when the task required the subjects to keep attention at the same retinotopic location as the spatial cue, the spatiotopic representation of the cue was not facilitated, only a strong retinotopic benefit was found right after the saccade(Golomb, Chun and Mazer, 2008). The authors suggested that the native coordinate or low-level representation of spatial attention is retinotopic, and argued against the role of a spatiotopic reference frame across a saccade (also see (Golomb, Nguyen-Phuc, Mazer et al., 2010; Golomb, Pulido, Albrecht et al., 2010; Golomb, Marino, Chun et al., 2011; Golomb and Kanwisher, 2012)).

2.4 Attentional pointer theory

Cavanagh and colleagues challenged the shifting receptive field and spatiotopic frame theory. They argued that remapping was the transfer of activation in the retinotopic priority map to predict the incoming stimulus due to saccades, which was similar to the finding that the neurons in the somatosensory area responded to the stimulus that was approaching (but not touching) the corresponding part of the body (MacKay and Crammond, 1987). In particular, they argued that remapping represented the updating of the 'attentional pointer' – top-down attention modulation in priority maps (e.g. SC, FEF, LIP), across saccades; then, this 'attentional pointer' updating in brain areas containing priority maps transferred to the corresponding neurons in lower visual areas (figures 4&5). They suggested that the attended locations were the most important information for tracking the objects and maintaining visual stability, and that feature information was not remapped and could be updated after saccades. They provided several lines of evidence to support attention remapping. The first experiment used the phenomenon of apparent motion. When a dot or an object disappears in one place then appears at another location in the visual field, it seems like the dot or objects are moving from the first to the second location, even though there is no physical movement, only two dots or objects flashing at different locations. They argued that the perceptual apparent motion phenomenon was a consequence of attention being dragged from the first location of the stimulus to the second location, thereby linking the two locations together as if a single stimulus was changing locations, i.e. moving (Cavanagh, Hunt, Afraz et al., 2010a). Besides, when a saccade is made between the two stimuli (or two locations), apparent motion is seen spatiotopically rather than retinotopically (Rock and Ebenholtz, 1962), i.e. they argued that '*the attention pointer to the pre-saccadic location is currently shifted to the target's expected post-saccadic location, enabling the detection of the target displacement as apparent motion in world coordinates*' (Cavanagh, Hunt, Afraz et al., 2010a, Page: 151).

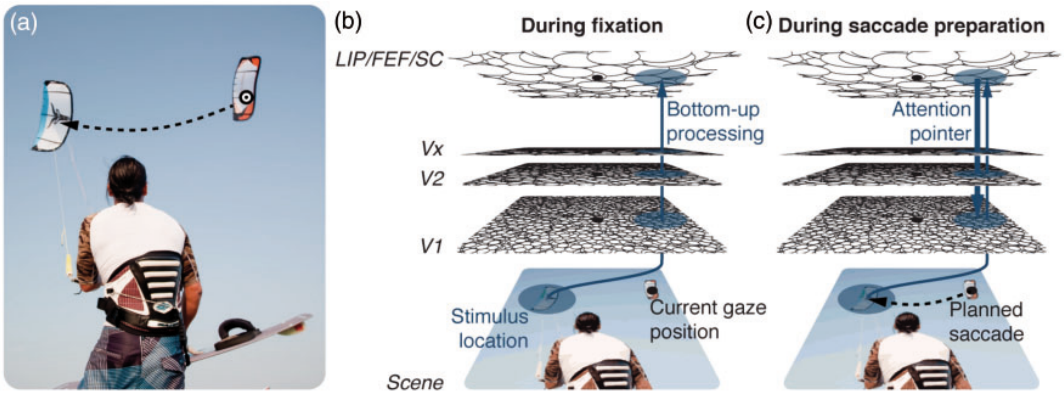

Figure 4. The illustration of attentional pointers. **(a)** The kite surfer is fixating on the red kite; and the blue kite will be his next saccade target. **(b)** The hierarchy of the visual system processing the visual scene, with each visual area retinotopically organized. The early stages (V1 to Vx) encode feature information, and late stages (such as LIP, FEF, SC) include a priority map of the current scene. **(c)** When a stimulus becomes more salient (here, the blue kite as the next saccade target) in the priority map, activity will increase at the corresponding location and a feedback signal will be sent to earlier visual areas. The activity in the priority maps may thus be treated as an attention pointer that indexes the corresponding locations in early visual areas (Adapted from Rolfs, 2015).

Rolfs and colleagues (2011) tested attention remapping in human subjects using a double-step saccade paradigm. The subjects were asked to do two tasks: plan a sequence of two saccades indicated by the central cue before the actual eye movement, and discriminate and report the orientation of a target tilted grating. The discrimination task could be at the first and second saccade target locations, or the task irrelevant control location, furthermore, it also could be at the remapped location of the second saccade target, which depended on the saccade direction and amplitude. The results showed that, before saccade, in addition to a performance improvement at the first and second saccade target locations, discrimination performance was also improved at the location of the remapped location of the second saccade target, which corresponds to the retinotopic region that the second saccade target will occupy after the first saccade. Based on these results, the authors suggested that, briefly before saccades, attention was shifted to those retinal locations that the task-relevant target would occupy once the saccades had been executed, which would facilitate and speed up later eye movements before the eyes started to move. A similar performance improvement at the remapped location of a task-relevant target was found in a masking paradigm (Hunt and Cavanagh, 2011) and a covert attention experiment (Jonikaitis, Szinte, Rolfs et al., 2013; Szinte, Carrasco, Cavanagh et al., 2015).

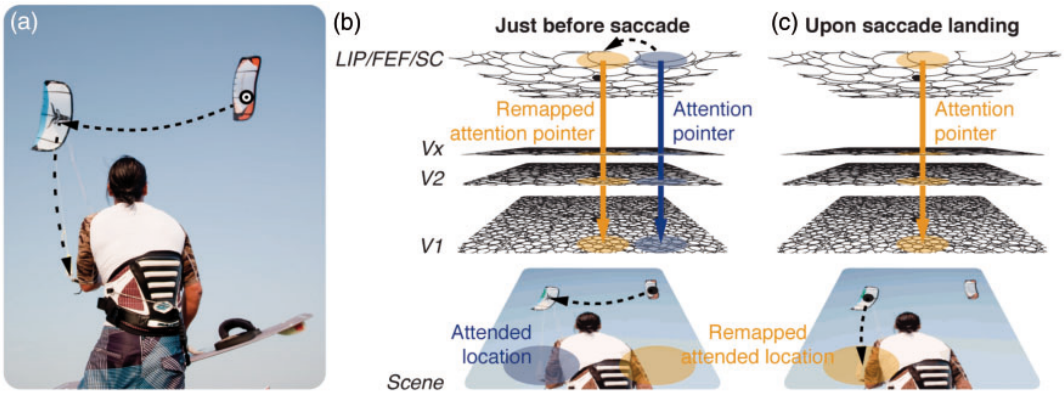

Figure 5. Attentional pointers update across saccades. **(a)** The kite surfer plans to make a saccade from the red kite to the blue kite and then a second saccade to the handle of his kite. **(b)** The handle (the second saccade target) attracts attention before the first saccade onset. The priority map is updated by increasing the activity of the corresponding neurons (yellow shade) that will process the handle after the saccades. This predictive remapping as an attention pointer then transfers to earlier visual areas (yellow arrow). **(c)** Right after the second saccade offset, the relevant neurons in the visual areas are modulated by attention as a consequence of this remapping (Adapted from Rolfs, 2015).

However, the physiological evidence supporting this theory is very limited, with most of the evidence based on human behavioral studies. The results of previous neuronal physiological work is difficult to interpret, as it is hard to distinguish whether the object was remapped or only attention was remapped. More neuronal physiological studies are necessary to link the behavioral and physiological evidence.

2.5 Remapping towards saccade target

Recently, Zirnsak and Moore (2014) provided an alternative proposal to explain remapping activity. They argued that the pre-saccadic remapping found in visual and visuomotor cortex and the perceptual changes accompanying saccades result from the selection of the saccade targets rather than an anticipation of the retinal image displacement (Zirnsak and Moore, 2014; Zirnsak, Steinmetz, Noudoost et al., 2014).

In traditional studies, the classical remapping experimental paradigms were more or less the same as the original Duhamel et al study (1992): a probe stimulus was presented either

in a neuron's current RF or in the post-saccadic/future RF. A neuron was considered to show predictive remapping activity or a receptive field shift if the neuron responded to the probe stimulus presented in the neuron's future RF immediately before a saccade. However, previous studies never investigated the dynamics of the RF shift and other changes in RF properties, such as the size of the RF around the time of a saccade. Zirnsak and Moore (2014) used the same classical paradigm, but mapped the FEF neuron's RF long before a saccade, long after a saccade, and around the time of a saccade. This allowed a more detailed measurement of the spatial properties of the FEF neuron's RF. Nevertheless, the authors found that the FEF neurons' RFs did not remap to the post-saccadic RF/ future RF before a saccade. Instead, the FEF neurons' RFs massively converged toward the saccade target. The authors suggested that FEF neurons collectively selected the location occupied by the saccade target, rather than predicting the consequence of the saccade. The authors suggested that the neuron's RF shift to the post-saccadic RF found in previous studies was because the pre-saccadic RF of some neurons overlapped to some degree with the hypothetically remapped RF, i.e. the future RF.

To better distinguish the classical predictive remapping and convergent RF shift in human subjects, Zirnsak et al (2011) modified the TAE paradigm used by Melcher (2007) and Biber and Ilg (2011). The authors placed the adaptor away from the initial fixation point and saccade target, instead of presenting it close to the fixation point. The test was placed either close to the saccade target or at the location corresponding to the same retinotopic location of the adaptor after saccade. If the neurons' RFs were predictively remapped, the TAE should increase when the test was placed at the same retinotopic location after saccade. By contrast, if the neurons' RFs shift to or converge onto the saccade target, the TAE should be increased when the test was placed close to the saccade target compared to when the test was placed at the same retinotopic location after saccade. The authors observed the second effect. Based on these results, they argued that previous remapping results could be explained by RFs converging toward the saccade target, which was consistent with the monkey physiological data they obtained in FEF (Zirnsak, Gerhards, Kiani et al., 2011). However, the number of the subjects was very low, with only 3 subjects participating including 2 of the study authors. More experimental evidence is therefore necessary to support this idea.

In a recent study in V4 (Neupane, Guitton and Pack, 2016)the authors found that RFs shift towards a saccade target for some neurons, but that other neurons' RFs shift towards post-saccadic RFs (or future receptive fields (FFs) in their study), and yet other neurons showed both types of remapping at different latencies. They found remapping towards the saccade target depended strongly on the relationship between saccade direction and the location of the RF. If saccades were directed towards the visual hemi-field covering the RF, remapping towards the saccade target was mainly observed. On the other hand, the other type of remapping, towards the post-saccadic RF, was independent of saccade direction.

2.6 Eye-position gain fields

Eye-position gain fields refer to the modulatory influence of eye-position or gaze-angle on the visual response of neurons in some brain areas. It provides a possible neuronal mechanism for creating a spatiotopic reference frame by moving the eyes while viewing the environment. Gain fields have been reported in almost all visual and visuomotor areas, as well as in some subcortical areas such as LGN and SC (Lehky, Sereno and Sereno, 2015). Gain fields code the spatiotopic location of a stimulus across a population of neurons rather than in single neurons. The spatiotopic information is obtained by the activity pattern of a group of neurons, from which the spatiotopic reference frame of the stimuli is built. The gain fields containing a self-induced image change on the retina are taken into account by the brain to build a stable representation of the visual environment. This may play a central role in the spatial constancy of visual perception. The time courses of gain fields were investigated in several brain areas (Morris, Kubischik, Hoffmann et al., 2012; Morris, Bremmer and Krekelberg, 2013, 2016) and it was found that gain fields in the dorsal visual stream are accurate and fast, with some signals even capable of predicting the future eye position (Morris, Bremmer and Krekelberg, 2016). However, another study reported that the gain fields in LIP alone were too slow to localize a briefly flashed target location in space after saccade (Xu, Karachi and Goldberg, 2012).

3 The middle temporal area (MT)

The middle temporal area (MT or V5) is located at posterior bank of the superior temporal sulcus (STS). It is one of the brain regions in the dorsal visual pathway and is highly involved in visual motion processing, but 'MT plays a richer and more varied role in vision' ((Born and Bradley, 2005), page: 158) than just motion perception alone. MT receives its major inputs from V1 (specifically from layer 4B), but also receives feed-forward inputs from the lateral geniculate nucleus (LGN), V2, V3, V3A, VP and PIP; besides, it receives feedback/modulatory inputs from higher level cortex such as FEF and LIP (Maunsell and van Essen, 1983c; Felleman and Van Essen, 1991; Sincich, Park, Wohlgemuth et al., 2004). One of its major projection regions is the medial superior temporal area (MST). MT is a retinotopically organized region region, and every visual neuron in this area has a certain receptive field (RF) occupying a part of the contralateral visual hemi-field when the eyes keep fixation on a central point. Each MT area in the two hemispheres contains an approximately intact map of the contralateral visual hemi-field (Born and Bradley, 2005). About half of the MT neurons' RFs are in the central 15 degrees of the visual field (Van Essen, Maunsell and Bixby, 1981). Visual responses of MT neurons have five basic tuning properties (Maunsell and Van Essen, 1983b, a; Born and Bradley, 2005): 1) retinal position (due to the specific RF); 2) stimulus size (because of surround suppression effects); 3) binocular disparity; 4) motion direction and 5) motion speed of the stimuli in the RF. In terms of remapping, a previous of study has shown that the MT neurons do not show predictive remapping(Ong and Bisley, 2011); therefore, in this thesis, we will focus on the other type of remapping, the post-saccadic memory trace.

Based on these properties of MT neurons, and especially the retinotopic organization and appropriately small size of the RF, motion direction tuning, as well as the effect of top-down attention modulation on MT neurons (Treue, 2001, 2003; Busse, Katzner and Treue, 2008; Daliri, Kozyrev and Treue, 2016), we decided to record from MT. The retinotopic organization makes it an ideal area to investigate the shift of attention modulation and remapping across a saccade; and the appropriate size of MT neuronal RFs makes it possible to clearly delineate regions outside the RF. Moreover, the monkeys do not have to make big saccades. Therefor, MT is an ideal area to investigate the neuronal dynamics of attention shifts across saccades and trans-saccadic remapping properties such as feature tuning in the remapped response. In this thesis, we focused on these two issues by

recording from MT neurons when the monkeys were trained to perform a saccade along with an attention task.

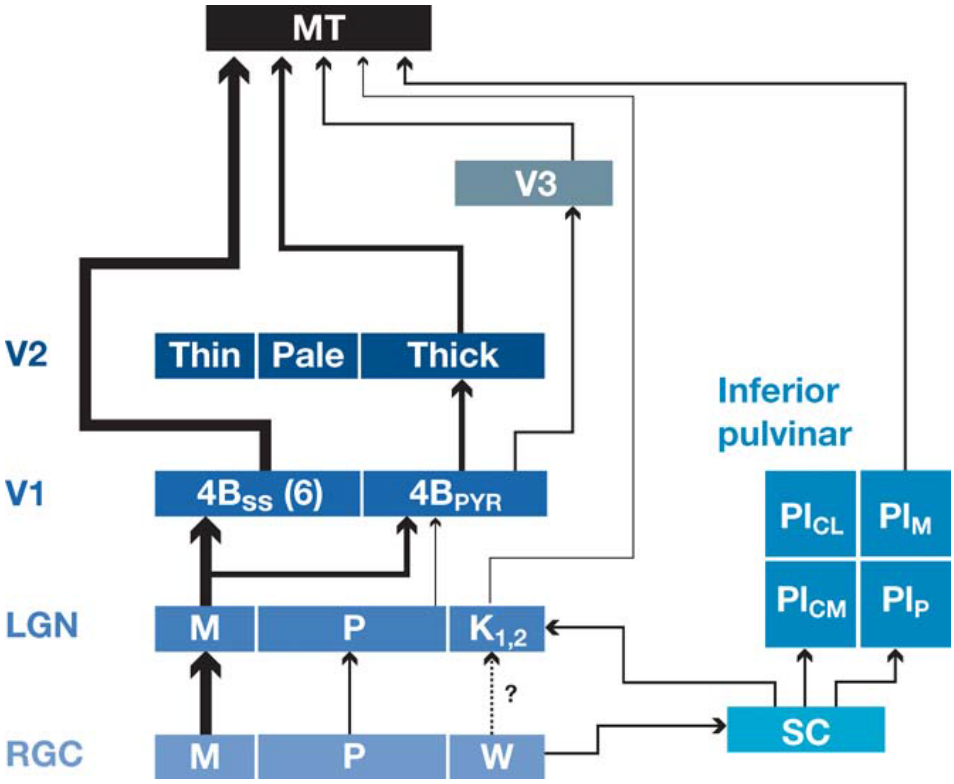

Figure 6. A map of the major projections into MT. Line thickness roughly represents the strength of the projection. The thickest lines indicate that the major direct input into MT is from V1. Abbreviations: $4B_{SS}$, spiny stellate neurons in layer 4B; $4B_{PYR}$, pyramidal neurons in layer 4B; LGN, lateral geniculate nucleus; M, magnocellular stream; P, parvocellular stream; K, koniocellular layers of LGN; PI_{CL}, central lateral nucleus of the inferior pulvinar; PI_{CM}, central medial nucleus of the inferior pulvinar; PI_{M}, medial nucleus of the inferior pulvinar; PI_{P}, posterior nucleus of the inferior pulvinar; RGC, retinal ganglion cells; SC, superior colliculus; VP, ventral posterior area. (Adapted from Born and Bradley, 2005)

4 General summary

In this thesis, at first, we studied a very critical and natural phenomenon, namely, maintaining attention on a spatially stable target across saccades. We recorded from well-isolated neurons in MT while the monkeys performed an attentional task. We investigated

the dynamics of how attention stopped modulating a neuron's response when a saccade brought a target out of its RF in Experiment one, and we also investigated the dynamics of how attention starts to modulate a neuron's response when a saccade brought a target into its RF in Experiment two. We also investigated human performance around the time of saccade as well; we focused on the dynamics of performance recovery after the saccade.

In the second part of this thesis, we investigate some important properties of remapping. Remapping has been reported and researched intensively in the last decades in both non-human primates and human subjects. However, there are still many debates on this topic, such as whether visual features and unattended objects are remapped across saccades. In this thesis, we designed and performed several experiments to investigate the perceptual and neural properties around the time of saccades to better understand remapping across saccades. At first, we will ask whether a remapped response can be found in MT. If the answer is yes, more importantly, we will investigate the modulation of top-down attention on the remapping response, and at the same time, we will investigate whether visual features are remapped across a saccade. Our study will provide important evidence to illuminate the debates on this topic, and contribute new insights into understanding what remapping is *per se.*

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Abbreviations

BOLD: blood-oxygenation level dependent

CD: corollary discharge

EEG: electroencephalography

FEF: frontal eye field

fMRI: functional magnetic resonance imaging

LFP: local field potential

LGN: lateral geniculate nucleus

LIP: lateral intraparietal area

MAE: motion after effect

MD: medial dorsal

MEG: magnetoencephalography

MST: medial superior temporal

MT: middle temporal

RDP: random dot pattern

RF: receptive field

SC: superior colliculus

STS: superior temporal sulcus

TAE: tilt after effect

TMS: transcranial magnetic stimulation

Chapter 2

Attentional remapping in macaque area MT is well-synchronized to saccades

Attentional remapping in macaque area MT is well-synchronized to saccades

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Summary

Humans and monkeys are able to keep track of relevant visual stimuli while making scanning saccadic eye-movements. Maintaining top-down attention on a relevant stimulus across saccades necessitates a rapid, saccade-synchronized remapping of attentional modulation from the target population representing the stimulus before the saccade to the one representing it after the saccade. Currently, the time-course of remapping is unknown. We trained two monkeys to make a saccade while maintaining top-down attention at a fixed spatial location. Recording from visual area MT, we find that attentional remapping is temporally well-sychronized to the saccade. Attentional modulation crosses over from the pre-saccadic to the post-saccadic target population at 31 and 52 ms after saccade offset in the two monkeys. Taking response latency into account, attentional remapping is well-timed to maintain top-down attention on relevant stimuli, so that they can be tracked and rapidly processed across saccades.

Introduction

Humans and monkeys are able to keep track of relevant visual stimuli while making saccadic eye-movements to scan a visual scene . Since the visual system mostly operates using retinotopic representations (Wurtz, 2008; Cavanagh et al., 2010; Marino and Mazer, 2016), in each visual area, a relevant visual stimulus (the target) at a fixed spatial location is represented by one neuronal population before the saccade and a different neuronal population after the saccade: we refer to these as the pre-saccadic target population and the post-saccadic target population respectively. As a result, to maximally and selectively enhance target processing (but not distractor processing) both before and after the saccade, a rapid, saccade-synchronized remapping of top-down attentional modulation from the pre-saccadic to the post-saccadic target population is optimal. Enhancement by top-down spatial attention would ideally be expected to be dominant at the pre-saccadic target population until just before saccade offset, and decay at or soon after saccade offset. Similarly, attentional enhancement would be expected to emerge at the post-saccadic target population at or soon after saccade offset. In other words, if attentional enhancement of the pre-saccadic target population decayed well before the saccade, or attentional enhancement of the post-saccadic target population emerged well after the saccade, there would be time-periods where the target stimulus did not receive the benefits of top-down attention. Contrariwise, if attentional enhancement of the pre-saccadic target population lingered after the saccade, or attentional enhancement of the post-saccadic target population emerged pre-emptively well before the saccade, attention would be peri-

saccadically allocated to irrelevant spatial locations, distractor processing would potentially be facilitated and this would be disadvantageous for task performance.

Until now, to our knowledge, the time-course of the remapping of top-down spatial attention from the pre-saccadic to the post-saccadic target population across a saccade has never been explicitly measured. In the only previous physiological recording study on this issue, using a mental curve-tracing task similar to ours with a fixed attentional target, top-down attentional enhancement of multi-unit activity in monkey V1 was reported to emerge in the post-saccadic target population approximately 80 ms after the end of the saccade (Khayat et al., 2004). However, this study did not measure the dynamics of the decay of attentional enhancement in the pre-saccadic target population. On the other hand, in a human imaging study, fMRI and EEG data from humans have been presented as evidence for lingering top-down attentional modulation for about 100 ms after the saccade in the pre-saccadic target population (Golomb et al., 2010a); this was supported by results from human psychophysical studies (Golomb et al., 2008; Golomb et al., 2010b). Human psychophysical data consistent with early, pre-saccadic emergence of top-down attentional modulation in the post-saccadic target population has also been reported (Rolfs et al., 2011; Szinte et al., 2015). This psychophysical inference of pre-emptive attentional modulation in the post-saccadic target population is consistent with a large body of single-neuron recording data from putative attentional control regions in monkeys showing that neurons in the lateral intraparietal area, superior colliculus and frontal eye field (Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg,

1997; Wurtz, 2008) respond predictively (and sometimes before the saccade) when a stimulus was expected in their RF after the saccade. This predictive activity is greater for stimuli with greater bottom-up saliency (Gottlieb et al., 1998; Joiner et al., 2011) and for stimuli that are learnt visual search targets (Phillips and Segraves, 2010; Mirpour and Bisley, 2012) or saccade targets (Gottlieb et al., 1998).

Though these results are suggestive (see Discussion), they do not address the time-course over which top-down attentional enhancement is remapped from the pre-saccadic to the post-saccadic target population across a saccade. In order to measure the time-course of attentional remapping, we trained two monkeys to make a saccade while maintaining top-down attention on moving random dot pattern at a fixed spatial location. We recorded from visual area MT, a key locus in the motion-processing pathway of humans and monkeys, where neurons show both small RFs and clear, robust, attentional enhancement (Treue and Maunsell, 1996, 1999; Busse et al., 2008; Yao et al., 2016a). We show for the first time that attentional remapping is well-sychronized to the saccade and that attentional enhancement crosses over from the pre-saccadic to the post-saccadic target population soon after saccade offset. We recently showed that in humans performing a similar task, top-down spatial attention is fully available at the task-relevant location within 30 milliseconds after the saccade (Yao et al., 2016b). Taking response latency into account (see Discussion), our results show that attentional remapping is well-timed to maintain top-down attention on relevant stimuli, so that they can be tracked and rapidly processed across saccades.

Results

Our task required monkeys to maintain attention on one of four RDPs while also making a saccade (Figure 1A). We recorded from neurons in area MT during this task. Since MT neurons have retinotopic RFs whose spatial location moves with each saccade, the attended target RDP lay in the RF of (and was therefore represented by) different populations of neurons before and after the saccade. In Experiment 1, we estimated the attentional enhancement of the pre-saccadic target population, while in Experiment 2, we estimated the attentional enhancement of the post-saccadic target population. To do this, in Experiment 1, *before* the saccade, we placed the attended RDP either in the RF (the target condition) or meridionally opposite to it (the distractor condition): we measured the attentional enhancement of the pre-saccadic target population by comparing the firing-rates in the target and distractor conditions. In contrast, in Experiment 2, *after* the saccade, we placed the attended RDP either in the RF (the target condition) or meridionally opposite to it (the distractor condition): we now measured the attentional enhancement of the post-saccadic target population by comparing the firing-rates in the target and distractor conditions. Based on prior findings (e.g. Treue and Maunsell, 1996, 1999), we expected to see an attentional enhancement of the pre-saccadic target population (in Experiment 1) before the saccade and of the post-saccadic target population (in Experiment 2) after the saccade. This is indeed what we found. In Experiment 1, the population average PSTH showed a greater response before the saccade when a target RDP, rather than a distractor RDP, appeared in the neuron's RF before the saccade (target condition: blue vs. distractor condition: red

curves in Figure 1B); the stimulus in the RF after the saccade was always a distractor. In Experiment 2, the population average PSTH showed a greater response after the saccade when a target RDP, rather than a distractor RDP, appeared in the neuron's RF after the saccade (target condition: blue vs. distractor condition: red curves in Figure 1B); the stimulus in the RF before the saccade was always a distractor. Both these effects were statistically significant. We defined and estimated the attentional enhancement as the difference in firing-rates between target and distractor conditions. For the pre-saccadic target population in Experiment 1, there was significant attentional enhancement in the time-window from 0-500 ms before saccade onset (Monkey H: mean difference = 5.2 ± 0.9 spikes/second, 11.5 % enhancement, $p<0.0001$; Monkey E: 5.9 ± 1.1 spikes/s, 31.3 % enhancement, $p<0.0001$), but not from 0-500 ms after saccade offset ($p>0.05$). For the post-saccadic target population in Experiment 2, there was significant attentional enhancement in the time-window from 0-500 ms after saccade offset (Monkey H: mean firing-rate difference between target and distractor conditions = 6.0 ± 0.9 spikes/second, 19.0 % enhancement, $p<0.0001$; Monkey E: 6.4 ± 1.1 spikes/s, 20.3 % enhancement $p<0.0001$), but not from 0-500 ms before saccade onset ($p>0.05$). Further, for both the pre-saccadic and post-saccadic target populations in both monkeys, the difference between the pre-saccadic and the post-saccadic attentional effects was also significantly different (all p-values < 0.001).

These results confirm, as expected, that attentional enhancement of firing-rate is found in the pre-saccadic target population before the saccade, and in the post-saccadic target population after the saccade. Our primary goal was

to characterize the time-course of this remapping of attentional enhancement from the pre-saccadic to the post-saccadic target population and how well this remapping of attentional enhancement was synchronized to the saccade. To do this, we focused on the time-interval from 200 ms before to 200 ms after saccade offset during which the attentional remapping takes place (Figure 2). For ideal task performance, the attentional remapping would take place as close to saccade offset as possible so that attentional enhancement would be greatest at the pre-saccadic target population until saccade offset and at the post-saccadic target population after saccade offset. We find that attentional enhancement of the pre-saccadic target population (Experiment 1) was statistically significant throughout the pre-saccadic period (-200 ms to 0 ms before saccade offset) and until 100 ms of saccade offset in monkey H and 50 ms in monkey E (grey curves in Figures 2A,B). The attentional enhancement of the post-saccadic target population (Experiment 2) became statistically significant after saccade offset in monkey H and after 50 ms of saccade offset in monkey E (black curves in Figures 2A,B). The attentional effect in the post-saccadic target population became larger than the attentional effect in the pre-saccadic target population at 31 ms (monkey H, IQR = 12 ms) and 52 ms (monkey E, IQR =12 ms) after saccade offset; we call this time the attentional cross-over time. The proximity of the attentional cross-over to saccade offset indicates that the attentional remapping is well-synchronized to the saccade, after taking the visual response latency of MT neurons into consideration (see Discussion). A direct statistical comparison of the attentional effects in Experiment 1 and 2 also confirmed this result. The attentional effect in the pre-saccadic target population (Experiment 1, grey curve in Figures 2A,B) was significantly greater than that in the post-

saccadic target population (Experiment 1, grey curve in Figures 2A,B) until saccade offset in monkey H and 50 ms after saccade offset in monkey E (two-sample t-test, one-sided p-value < 0.05). This effect then reversed: the attentional effect in the post-saccadic target population became greater than that in the pre-saccadic target population after 50 ms following saccade offset in both monkeys.

These results indicate that attentional remapping was well synchronized with saccade planning/execution. We examined the alternative possibility that attentional remapping and saccade planning/execution were both triggered by the cue to make the saccade, but proceeded independently. If attentional remapping and saccade planning/execution proceed independently, then relative to saccade offset, the time-course of attentional remapping would be delayed for trials with short-latency saccades compared to trials with long-latency saccades. On the other hand, if attentional remapping and saccade planning/execution are indeed synchronized with each other, then the time-course of attentional remapping would be similar for short and long-latency saccades. At the same time, in this scenario, relative to the cue to make the saccade (i.e. the offset of the fixation point), attentional remapping would occur later on trials with long-latency saccades compared to short-latency saccades. We therefore plotted the time-course of attentional remapping aligned to saccade offset (Fig.3A,C) and fixation point offset (Fig.3B,D) for trials with saccade latencies shorter than the 33rd percentile and longer than the 66th percentile (solid and dashed curves respectively; also see Supplementary Figure 2). We found the pattern expected if attentional remapping was synchronized with saccade planning/execution. For both

Experiment 1 (Fig.3A,B) and Experiment 2 (Fig.3C,D), when aligned to saccade offset, the the remapping time-course for trials with long-latency saccades and trials with short-latency saccades was superimposed; consistent with the visual impression, the peak cross-correlation lag was at zero delay. Similarly, as expected, when aligned to fixation point offset (i.e. the cue to make the saccade), the remapping time-course for trials with long-latency saccades was delayed compared to the trials with short-latency saccades in both Experiment 1 and 2, with a peak cross-correlation lag of 50 ms. However, the pattern of a delay when aligned to fixation point offset is especially clear for the attentional enhancement of the post-saccadic population (in Experiment 2). In Experiment 1 (for the attentional decay in the pre-saccadic population), the delay remains clear at times after the mean saccade latency (Figure 3B), but the curves appear superimposed before that. It therefore remains possible that the early time-course of attentional decay in the pre-saccadic population was triggered by saccade offset, and then became co-ordinated with saccade execution in the post-saccadic phase. The data from individual monkeys, though noisy (because each curve now used only one-third of the trials from the corresponding task condition) was consistent with these general patterns (Supplementary Figures 3 and 4).

We considered two additional issues. First, we did not find any evidence for predictive attentional remapping in MT: there was no attentional enhancement of the post-saccadic target population before saccade offset (black diamonds in Figures 2A,B). This is particularly notable because unlike earlier studies (Ong and Bisley, 2011; Yao et al., 2016a), we made sure that there was a stimulus in the RF before the saccade. The presence of this

stimulus ensured a stimulus-driven response on which a putative predictive attentional signal could act, and rules out the argument that the apparent absence of a predictive response is simply because the predictive attentional signal does not modulate spontaneous activity in MT. Second, we considered the fact that in monkey E, the firing-rates of the neurons in both the target and distractor conditions is higher in Experiment 2 (Figure 2D) than in Experiment 1 (Figure 2F), even though two-sample tests did not show a significant difference. To rule out a potential influence of this difference on our estimate of the attentional time-course in monkey E, we dropped the 25 % of neurons with the highest overall firing rates in Experiment 2 and restricted the analysis to the remaining 75 % of neurons (Supplementary Figure 1). This procedure substantially equates the firing-rates in the two Experiments, but does not affect our conclusions. The attentional cross-over time now occurs at a median time of 56 ms (IQR =13 ms) after saccade offset (compared to 52 ms, IQR=12 ms in the full sample in Figure 2B).

Discussion

We report, for the first time, that attentional remapping is well-sychronized to the saccade: attentional enhancement crosses over from the pre-saccadic to the post-saccadic target population at 31 and 52 ms after saccade offset in the two monkeys. We recently showed that in humans performing a similar task, top-down spatial attention is fully available at the task-relevant location within 30 milliseconds after the saccade (Yao et al., 2016b). Given an onset latency of approximately 30 ms in MT (Bair et al., 2002), a visual change occurring 30 ms after saccade offset would reach MT by 60 ms after saccade offset, by which time attention would have crossed-over to the post-saccadic target population (as we show here). This rapid recovery of spatial attention following a saccade is also consistent with data from double-step saccades (Hallett and Lightstone, 1976) and visual search (McPeek et al., 2000) showing that successive saccades can be made with very short inter-saccadic intervals and therefore the target of the second saccade can be rapidly located after the first saccade. In our data, attentional enhancement of the post-saccadic target population emerged at saccade offset and within 50 ms of saccade offset in the two monkeys, compared to the 80 ms time (after the stimulus entered the post-saccadic RF) reported in a previous study of multi-unit activity in V1 in monkeys performing a mental curve-tracking task (Khayat et al., 2004). Given the uncertainty in estimating the RF edge during a saccade, the times in the two studies appear comparable (or possibly slightly earlier in MT). Also, in our data, attentional enhancement of the pre-saccadic target population lingered after the saccade and disappeared by 50 ms after saccade offset in one monkey and by 100 ms in

the other. This is consistent with previous human psychophysical and imaging evidence suggesting that a lingering attentional modulation of the pre-saccadic target population for about 100 ms after saccade offset (Golomb et al., 2008; Golomb et al., 2010a; Golomb et al., 2010b). The lingering attentional modulation at the pre-saccadic neuronal population even after attentional effects have emerged at the post-saccadic neuronal population is reminiscent of similar effects observed in attentional switch experiments where monkeys covertly changed their locus of spatial attention while maintaining fixation: in that scenario, attentional effects emerge at the new locus of spatial attention (and the neuronal population encoding this locus) before attentional effects decay in the neuronal population encoding the preceding locus of attention (Khayat et al., 2006; Busse et al., 2008). The time taken to accomplish the attentional switch in these previous studies in V1, MT and LIP, which can be as short as 150-200 ms (Khayat et al., 2006; Busse et al., 2008; Herrington and Assad, 2009, 2010), is also comparable to the time-course of attentional remapping across a saccade in our task. Our analyses however showed that attentional remapping across a saccade is synchronized to saccade planning/execution and is not the result of a visual cue-induced attentional switch as in these previous studies. It is possible that covert volitional attentional switches during fixation may engage the same circuitry as attentional remapping across saccades. The close co-ordination between peri-saccadic attentional remapping and saccadic planning/execution may be facilitated by the overlapping neural circuitry mediating these two phenomena (Awh et al., 2006; Noudoost et al., 2010).

We did not find any evidence for attentional enhancement of the post-saccadic target population before the saccade, even though our experimental design ensured that there would be a distractor-driven response before the saccade on which an attentional effect could be seen, if present. This confirms results in two previous studies (Ong and Bisley, 2011; Yao et al., 2016a) where no significant attentional modulation of spontaneous activity was found in MT neurons before the saccade. Similarly, in our recent human psychophysical study using a stimulus paradigm very similar to the one here, we did not find any evidence for a predictive, pre-saccadic shift of attention to the post-saccadic target population (Yao et al., 2016b). In contrast, a large body of single-neuron recording data from putative attentional control regions in monkeys shows that neurons in the lateral intraparietal area, superior colliculus and frontal eye field (Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg, 1997; Wurtz, 2008; Mirpour and Bisley, 2016) as well as some ventral stream areas (Nakamura and Colby, 2002) respond predictively (and sometimes before the saccade) when their RF was stimulated before the saccade, but not after the saccade. Though this anticipatory activity has not been studied explicitly in conditions evoking top-down spatial attention, predictive activity is greater for stimuli with greater bottom-up saliency (Gottlieb et al., 1998; Joiner et al., 2011) and for stimuli that are learnt visual search targets (Phillips and Segraves, 2010; Mirpour and Bisley, 2012) or saccade targets (Gottlieb et al., 1998). Human psychophysical data consistent an with early, pre-saccadic emergence of top-down attentional modulation in the post-saccadic target population have also been reported (Rolfs et al., 2011; Szinte et al., 2015). We hypothesize that the anticipatory remapping seen in attentional and oculomotor control

areas like LIP, FEF and SC is part of the process that enables attentional remapping in MT that is well synchronized to the saccade. In other words, even though this process starts before the saccade in these areas, its effects in MT, with which these areas are strongly connected (Maunsell and van Essen, 1983; Ungerleider and Desimone, 1986; Blatt et al., 1990), only manifest after the saccade. In this view, the previous results on trans-saccadic remapping represent the predictive, pre-saccadic shift of attentional pointers on a retinotopic map that keeps track of attended locations across saccades (Cavanagh et al., 2010), so that attended locations can be preferentially processed with minimal delay after the saccade (Yao et al., 2016a). This reduction of delay would be especially helpful when planning rapid sequential saccades and could also help maintain an uninterrupted visual experience across saccades. While additional evidence from other visual areas (for example, in the ventral stream) and using other visual stimuli are undoubtedly needed to resolve these issues, the physiological data here, combined with our recent human psychophysics results (Yao et al., 2016b) support our hypothesis that spatial attention and saccadic processing co-ordinate well to ensure that relevant locations are attentionally enhanced soon after the beginning of each eye fixation, and can be tracked and rapidly processed across saccades.

Experimental Procedures

Our description of the Methods here is similar to that presented in our previous publication (Yao et al., 2016a), since the general experimental procedures are the same. We trained two male rhesus monkeys (Macaca mulatta, 7–11 kg), monkey H and monkey E, to perform a demanding visuospatial-attention task along with a saccade. Each monkey was implanted with a titanium head holder to minimize head movements during the experiment. One recording chamber was also implanted in each monkey above the left (monkey E) or the right (monkey H) parietal cortex to allow access to MT, with implantation locations chosen based on a preceding MRI scan. All procedures were approved by the district government of Lower Saxony, Germany, and all surgeries were conducted under general anesthesia using standard techniques.

The experiments were performed in a dimly-lit room with the only source of light being the display monitor. A CRT monitor (Sony Trinitron GDM-FW900) at a distance of 57 cm from the monkey was used to display the visual stimulus at a refresh rate of 76 Hz and a spatial resolution of 40 pixels/degree. The monkey sat in a custom-made primate chair during the experiment. Stimulus presentation, reward delivery, electrophysiological and behavioral data collection was controlled by custom software and run on an Apple Macintosh computer. All stimulus onsets and durations were specified in terms of number of frames (CRT monitor refreshes), and the stimulus presentation times reported here in millisecond units are correct to within 13 ms (the duration of one frame), given the vertical scan-rate properties of the

CRT monitor. The animals received a fluid reward immediately following each correct trial. The eye-position was monitored by an EyeLink 1000 (SR Research, Canada) system at 1000 Hz. Neuronal activity was recorded extracellularly with a 5-channel micro drive system (Mini Matrix, Thomas Recording, Giessen, Germany) and processed using the Plexon data acquisition system (Plexon Inc., Dallas, TX). Only data from well-isolated neurons were used for the analysis. MT was identified by referencing the recordings to the structural MRI and by the physiological properties of the recorded neurons: most neurons were direction-tuned, the average diameter of the receptive fields (RFs) was approximately equal to the RF eccentricity and there was a predictable progression of RF centers at different locations along the superior temporal sulcus.

Behavioral tasks and stimuli

Once a neuron was isolated, we had the monkey perform a fixation task where the monkey had to maintain fixation on a fixation point and respond to a brief luminance change at the fixation point. During this fixation period, we located the RF by moving a stationary circular random dot pattern (RDP) across the screen using a mouse. We then determined the neuron's preferred direction and speed during the fixation task by presenting a RDP with moving dots within a circular aperture in the RF, changing the direction and speed every 250 ms to a value picked from a set of 3 possible speeds (4, 8 or 16 degrees per second) and 12 possible directions (evenly separated by 30 degrees around a circle). For the main experiment, we used stimuli

with directions and speeds equal or close to the preferred direction and the preferred speed thus determined.

After identifying the RF location and preferred direction, we switched to the main experiment (Figure 1), where the monkey performed an experimental "attention-saccade" task (either Experiment 1 or Experiment 2) and a control task in a pseudo-randomly interleaved manner. In the experimental task, comprising 80 % of trials, the monkeys were trained to concurrently perform a visuospatial attention task and a saccade task on each trial: they were instructed to pay attention to the target RDP and make a saccade if the fixation point jumped to a new location. The monkeys initiated the trial by holding a metal bar and foveating a black fixation point. After 118 ms of fixation, to indicate the location of the upcoming target RDP, a stationary circular RDP cue (of the same size as the target) was presented for 263 ms. After an additional delay of 329 ms following cue offset, four moving RDPs (2 degrees in radius, all dots moving at or close to the neuron's preferred direction of motion and within stationary circular apertures) were presented on the screen. Two of the RDPs were presented in the neuron's pre-saccadic and post-saccadic RFs respectively and the other two RDPs were located opposite to these stimuli (i.e. reflected across the horizontal or vertical meridian, see Figure 1). The monkeys' task was to respond to a brief (132 ms) direction change in the RDP at the previously cued location (the target) by releasing the metal bar (within 600 ms of the change), but ignore similar changes in the distractor (the RDP opposite to the target). Trials terminated 600 ms after the target change, with the monkey receiving a drop of juice if the bar had been correctly released during this period. In addition, during the

trial, if the fixation point jumped to a new location, the monkeys had to re-fixate the fixation point while continuing to attend to the cued target. The direction change in the target RDP could occur between 263 ms to 1973 ms after RDP onset. Distractor changes occurred on about 37 % of trials and never more than once on each trial. The timing of distractor changes overlapped that of target changes, with the additional requirement that any distractor change occurred at least 500 ms before the target change on each trial. This separation ensured that the monkeys' rare responses to the distractor change could be easily identified and distinguished from their responses to the target change. The fixation point jumped to its new location (and became the saccade target) 1382 ms after fixation point onset (i.e. 671 ms after RDP onset); however, this event did not occur if the trial had terminated by then (either by a correct or incorrect bar-release or by a missed target change). The saccade target then stayed on for 1368 ms (or until the end of the trial). There was a one-frame (13 ms) overlap between the fixation point and the saccade target, so that the fixation point disappeared one frame after the saccade target appeared: perceptually, the fixation point appeared to jump from its original location to the saccade target. Once the fixation point jumped, the monkey had to make a saccade to the new location of the fixation point within 263 ms and maintain fixation until the end of the trial. The saccade target appeared between 10 and 20 degrees eccentrically (value fixed for each neuron, and either 15 or 20 degrees in most cases). Saccades were always either horizontal or vertical. We used a fixed and predictable time for the fixation point jump to reduce the temporal uncertainty about when the fixation point would jump and thereby minimize the monkeys' need to monitor the fixation point or saccade target

location in order to detect the saccade jump. This would enable the monkeys to better focus their attention on the target RDP. The median saccade latency was 136 ms in monkey H and 142 ms in monkey E; 99 % of the saccades occurred before 217 ms in monkey H and 229 ms in monkey E.

In Experiment 1, the cue (and by extension, the target RDP) was located either in the neurons' pre-saccadic RF (attend-in condition) or opposite to it (attend-out condition) equally often in a pseudo-randomly interleaved manner. Experiment 2 was similar, except that the cue (and by extension, the target RDP) was located either in the neurons' post-saccadic RF (attend-in condition) or opposite to it (attend-out condition) equally often in a pseudo-randomly interleaved manner. The control task, comprising 20 % of trials, was a 'simple-saccade' task where the monkey simply made a saccade when the fixation point jumped to a new location and maintained fixation till the end of the trial to obtain the juice reward. There was no concurrent attentional task; i.e. no cue and no moving RDPs were presented. Data from this control task were only used to select visually-responsive neurons for further analysis (see below).

In all the tasks, the background was always grey with a luminance of 14.2 cd/m^2, and the fixation point and RDPs including the stationary cue were black with the luminance of 0.68 cd/m^2. Individual RDP dot size was 0.1° x 0.1°, and the dot density was 10 $dots/deg^2$. Monkeys had to maintain fixation within a circular window of 2 degrees radius around the fixation point before the fixation point jumped. Following a period of 263 ms after the fixation point jumped (which gave the monkeys time to make the saccade), the monkeys

had to maintain fixation within a circular window of 3 degrees radius around the saccade target. This larger post-saccadic window was not necessitated by fixation inaccuracy, but rather by across-trial drifts in calibration: using a window centered on the median eye-position within the trial, the maximal within-trial deviation was less than 2 degrees in over 95 % of trials. The saccade direction was set according to the position of the RF: for example, if the RF center was directly above or below the fixation point, we used a horizontal saccade, while if the RF center was directly to the left or right of the fixation point, we used a vertical saccade. If the RF center was offset both vertically and horizontally from the fixation point, the choice was no longer critical, but we usually used a horizontal saccade.

Data Analysis

All data analysis was performed using custom software in MATLAB (MATLAB Inc, Natick, MA). We detected saccades using a velocity-threshold criterion that was validated by visual inspection. onset (and offset) times were determined by when the eye velocity exceeded (and then dropped below) 100 degrees per second. This threshold value was set to lie clearly above the peak excursions of the baseline noise in the eye-velocity traces, and the algorithm was validated by visual inspection for each monkey. By considering the saccade to have ended when the velocity dropped below a threshold value well above the baseline noise (and when the eye was still moving), our threshold criterion provides a conservative, i.e. early definition of saccadic end-point and therefore if anything, a longer estimate of the cross-over time for attentional remapping.

We included data from all neurons that showed a visual response to the RDP in the RF both before and after the saccade. We identified these neurons as those that showed a significantly greater postsaccadic response (one-sided t-test, $p<0.05$, Bonferroni-corrected) in the attention-saccade task compared to the simple-saccade control in the time-periods 0 to 600 ms following RDP onset (i.e. they were visually responsive to the RDP in the pre-saccadic RF) and 0 to 600 ms following the saccade (i.e. they were visually responsive to the RDP in the post-saccadic RF). In total, out of 123 and 137 neurons recorded in Experiment 1 and Experiment 2 respectively, we analyzed 84 neurons in Experiment 1 (56 in monkey H and 28 in monkey E) and 84 neurons in Experiment 2 (52 neurons in monkey H and 32 neurons in monkey E). 29 neurons (all in monkey H) provided data for both Experiments 1 and 2. There were at least 9 trials for both the attend-in and attend-out conditions in Experiment 1 and at least 14 trials in Experiment 2 in all neurons. After excluding fixation breaks, monkey H performed the task correctly on 93.2 % of trials (with early “false-positive” releases on 3.7 % and “misses” on 3.1 % of trials), while monkey E performed the task correctly on 84.6 % of trials (with false-positive releases on 8.8 % and misses on 6.6 % of trials). We analyzed all correctly completed trials where the target change did not occur too close to saccade offset (i.e. the target change was at least 200 ms earlier or 200 ms later than saccade offset), since this was the time-period that we focused on to measure the time-course of attentional remapping.

Peri-stimulus time histograms (PSTHs) were calculated using non-

overlapping 25 ms time bins. The mean activity for each neuron across trials was first calculated and then these mean PSTHs for individual neurons were averaged across neurons to obtain the displayed PSTHs. In the attend-out conditions, to avoid the transient response to the brief change in the distractor stimulus within the receptive field, we excluded the period of 0 to 350 ms following the distractor change from the PSTH and firing-rate calculations. To calculate percentage changes in firing-rate when comparing two conditions, we first calculated a modulation index for each neuron as the difference in the firing-rates for the two conditions divided by their sum, averaged the modulation indices and then converted the average back into a percentage change. We used two-sided t-tests throughout unless mentioned otherwise; using the signed-rank test produced similar results. To calculate the attentional cross-over time, we used linear interpolation between data points to compute the time at which the black and grey curves (in Figures 2A, 2B and Supplementary Figure 1) crossed. To characterize the variability of this cross-over time, we used a bootstrap procedure where we randomly selected neurons with replacement to compute the attentional effect curves in the two experiments, computed the cross-over time and repeated this procedure 15000 times to generate a distribution of cross-over times. Since this distribution was skewed, we used the inter-quartile range (IQR) of this distribution to characterize the variability of the cross-over time. The median of the bootstrap distribution was very close in value to the cross-over time calculated from the original dataset. To estimate the delay between the difference curves in Figure 3 (and Supplemental Figure 3), we found the time-lag at which the cross-correlation reached a maximum value; this time-lag was consistent with the visual impression based on the graph.

Author Contributions

TY and BSK designed the study; TY conducted the experiments; TY and BSK analyzed the data; ST commented on the manuscript; TY and BSK wrote the manuscript.

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Figure Legends

Figure 1. Attention enhances different target populations before and after a saccade. A) Cartoon demonstrating that in a retinotopic representation, an attended stimulus is represented in different populations of neurons before and after a saccade. Therefore, to maintain attention on a stimulus while making a saccade, attentional effects must manifest in different populations of neurons before and after the saccade. B) Task-design and timing: Two rhesus monkeys were trained to perform a task that involved attending to one of four moving RDPs (the target) while also making a visually guided saccade if the fixation point (FP) jumped to a new location. An initial spatial cue marked the target location on each trial. The intervening saccade changed the spatial location of the neuron's RF so that a different RDP appeared in the RF before and after the saccade. In Experiment 1, the target RDP appeared before the saccade either in the neuron's RF or at the meridionally opposite location. In Experiment 2, the same happened after the saccade. Values next to each panel represent the durations of the task phase represented by that panel. For details, see Materials and Methods. C) Population average peri-stimulus time histograms (PSTHs) in Experiment 1 aligned to the time of saccade offset. After the saccade, the stimulus in the RF was always a distractor, while before the saccade, either a target (blue curve) or a distractor (red curve) appeared in the neuron's RF: the neurons respond more in the former case before the saccade. PSTHs plotted using 25 ms, non-overlapping bins. The inset rectangles depict the cue location for the two conditions. From left to right, the first dashed vertical line represents the mean time of RDP onset, the second dashed vertical line the mean time

of fixation point jump and the dotted vertical line the mean time of saccade onset. The early response before RDP onset in the attend-in condition (blue curve) is the response to the cue. Data pooled from both monkeys. D) PSTHs for Experiment 2, in format a similar to B. Before the saccade, the stimulus in the RF was always a distractor, while after the saccade, either a target (blue curve) or a distractor (red curve) appeared in the neuron's RF: the neurons respond more in the former case after the saccade.

Figure 2. Attentional remapping is well-synchronized to the saccade. A,B) The attentional cross-over time (when the attentional enhancement of the post-saccadic target population became larger than the attentional enhancement of the pre-saccadic target population) occurred at 31 ms (A, IQR = 12 ms, monkey H) and 52 ms (B, IQR =12 ms, monkey E) after saccade offset. Data for monkey H in A and for monkey E in B. Grey and black curves show the mean difference (and SEMs) between the target-in-RF and distractor-in-RF curves in Experiment 1 and Experiment 2 respectively (as shown in C-F), but plotted using 50 ms, non-overlapping time-bins. Diamonds above the curves indicate the successive, non-overlapping 50 ms time-bins in which the differences were significantly larger than zero (one-sided t-test): black diamonds for the black curve and gray diamonds for the gray curve. C-F) Same data as in Figure 1B (C-D) and Figure 1C (E-F), but plotted separately for the two monkeys and focusing on the time around the saccade (-200 to 200 ms relative to saccade offset); format otherwise identical. The gray curves in A and B are computed as the difference between the blue and red curves in C and D respectively, while the black

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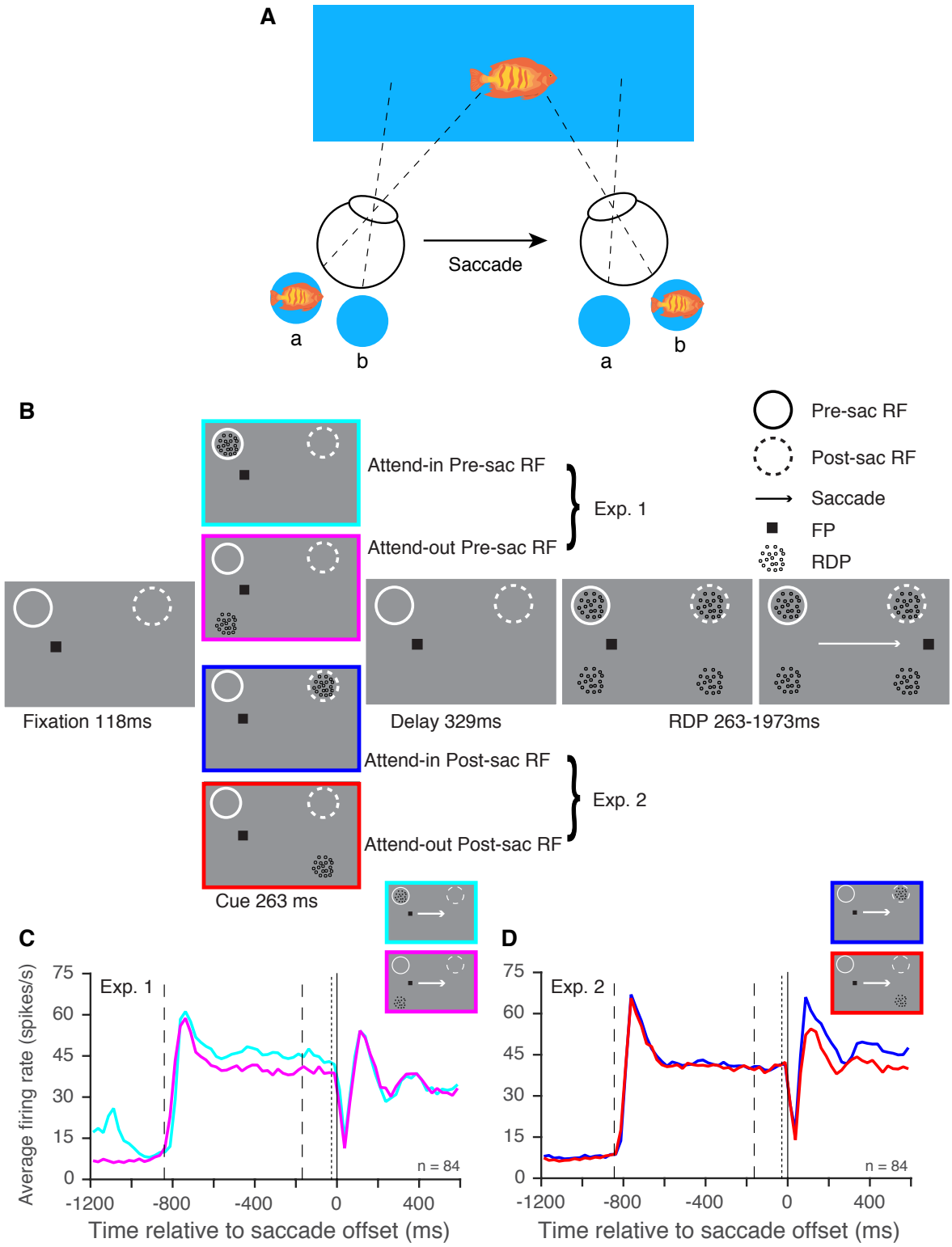
A
Saccade
a
b
a
b
B
Pre-sac RF
Post-sac RF
Saccade
FP
RDP
Attend-in Pre-sac RF
Attend-out Pre-sac RF
Exp. 1
Fixation 118ms
Delay 329ms
RDP 263-1973ms
Attend-in Post-sac RF
Attend-out Post-sac RF
Exp. 2
Cue 263 ms
C
Exp. 1
Average firing rate (spikes/s)
75
60
45
30
15
0
n = 84
-1200
-800
-400
0
400
Time relative to saccade offset (ms)
D
Exp. 2
75
60
45
30
15
0
n = 84
-1200
-800
-400
0
400
Time relative to saccade offset (ms)

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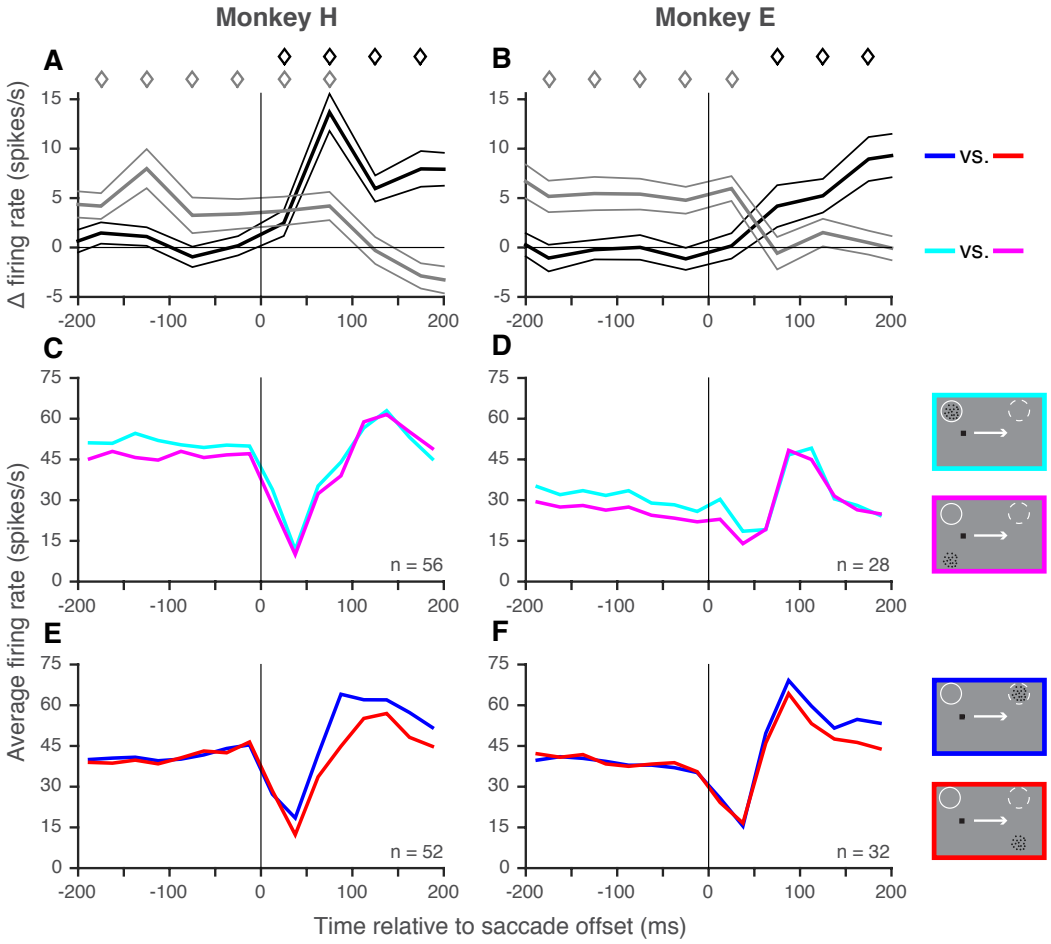

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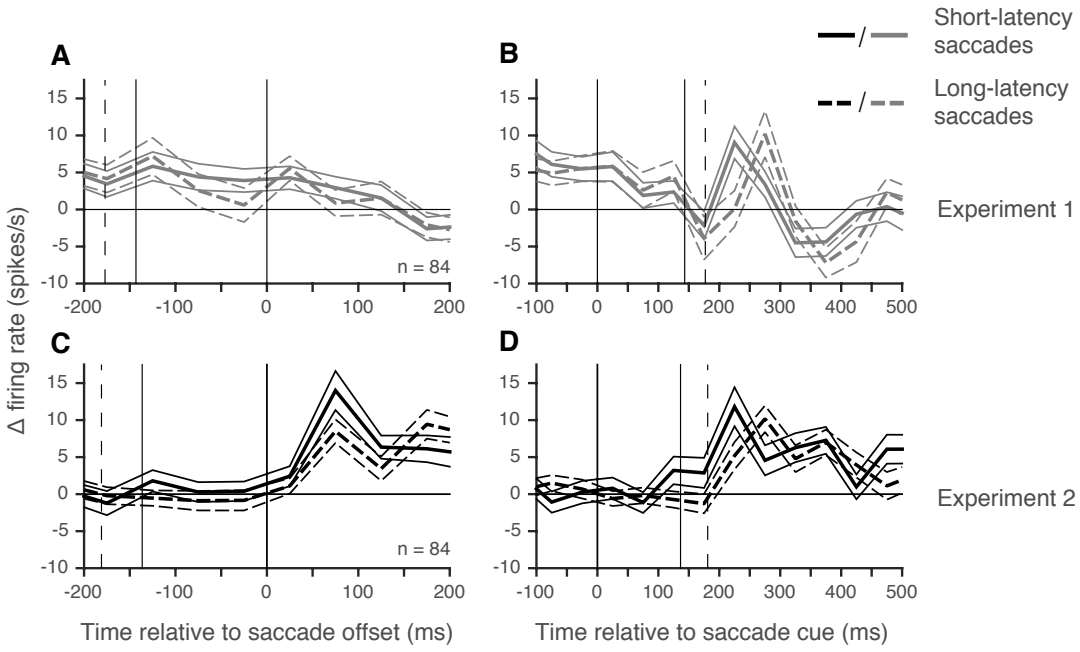

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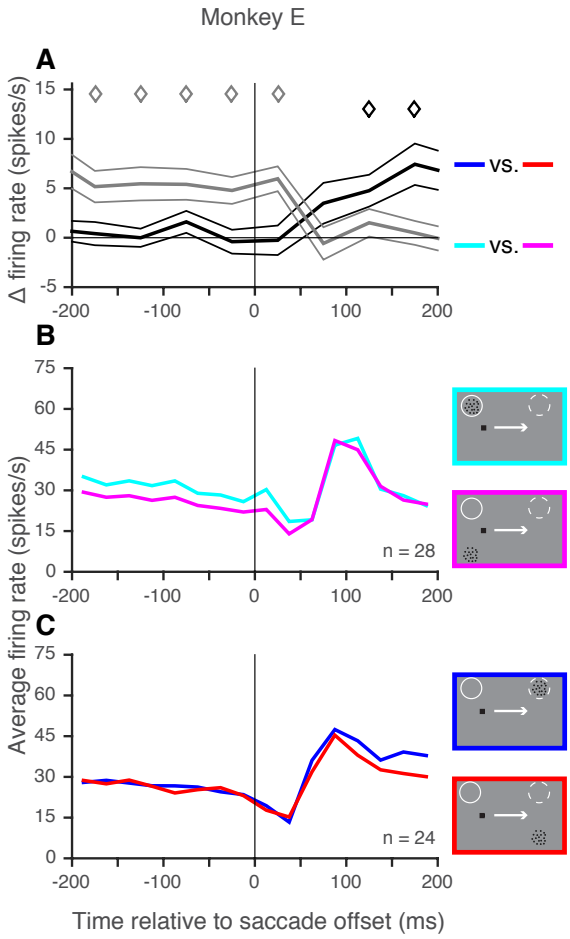
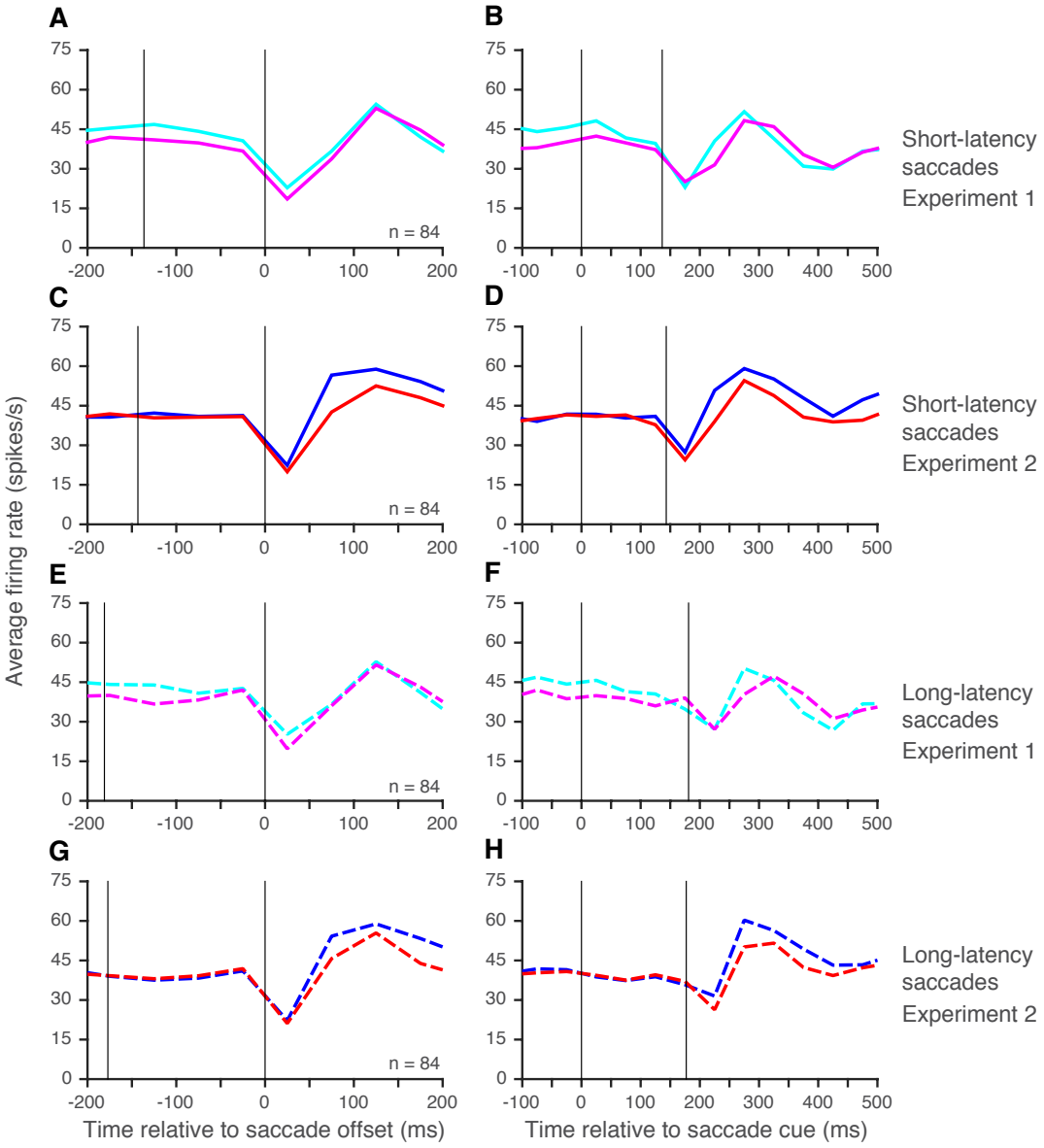
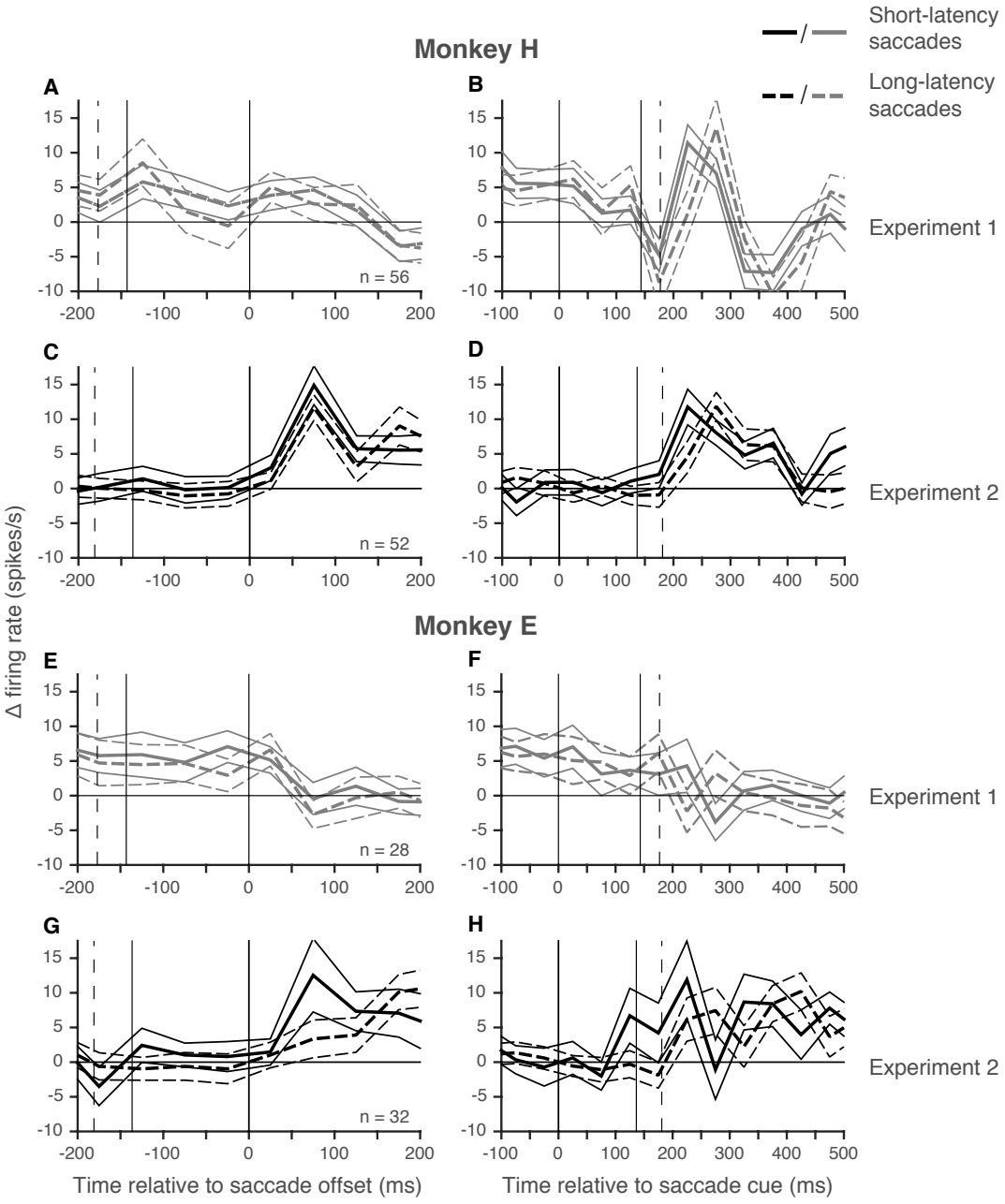


Supplemental Figure 1. Attentional remapping remains well-synchronized when the firing-rates are matched between the populations in Experiment 1 and 2 in monkey E. Related to Figure 2. Figure format identical to Figure 2, except that only data from monkey E are shown, and the 25 % of highest-firing rate neurons from Experiment 2 were excluded from the sample. The attentional cross-over time now occurred at a median time of 56 ms (IQR =13 ms) after saccade offset (compared to 52 ms, IQR=12 ms in the full sample in Figure 2B).

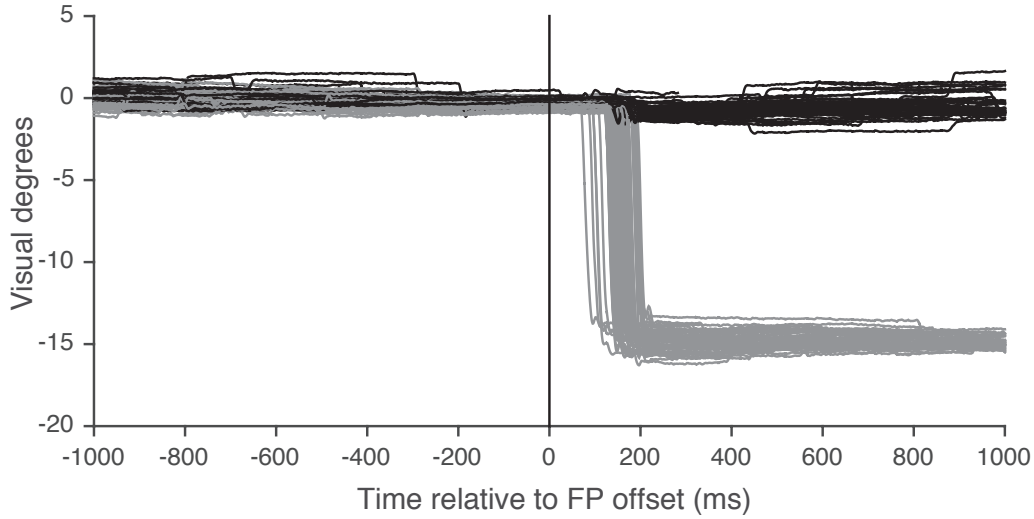


Supplemental Figure 2. The time-course of attentional remapping is similar when aligned to saccade offset, not fixation point offset. Related to Figure 3. PSTHs from which the difference curves in Figure 3A-D were derived. As in Figure 2, the difference curves use 50 ms non-overlapping time-bins, while the PSTHs use 25 ms non-overlapping time-bins. Data plotted for trials with saccade latencies shorter than the 33rd percentile (A-D) and longer than the 66th percentile (E-H) for the corresponding task conditions in Experiment 1 (A,B,E,F) and Experiment 2 (C,D,G,H). Left column shows data aligned to saccade offset and the right column shows data aligned to fixation point offset. Vertical lines away from 0 indicate the mean time of fixation point offset (left column) and the mean saccade latency (right column). Data from both monkeys were pooled for this analysis (see Methods).



Supplemental Figure 3. The patterns in the pooled data of Figure 3 are generally consistent with those in the individual monkeys. Related to Figure 3. Figure format identical to Figure 3, except that instead of the pooled data in Figure 3, data are shown separately for monkey H (A-D) and monkey E (E-H). The remapping time-course remained superimposed when aligned to saccade offset for both monkeys (A,C, E and G; estimated delay = 0 ms in all cases). When aligned to fixation point offset, the time-course of attentional enhancement of the post-saccadic population (in Experiment 2) in both monkeys showed the same delay pattern for long-latency saccade trials seen in the pooled data (estimated delay = 50 ms; D, H), as expected if attentional remapping was co-ordinated with saccade planning/execution. The time-course of attentional decay in the pre-saccadic population was more variable (C,G). Similar to the pooled data, monkey H showed superimposed curves at early times and a 50 ms delay later (from 200 ms after fixation point offset; C). However, monkey E did not show this delay: the attentional decay in the pre-saccadic population even appeared to be earlier (with a peak lead of 50 ms) in trials with longer-latency saccades (F).

Additional supplementary materials 1: Example eye traces



The example eye traces of trial No. 80-180 from Monkey E in the experiment 1 when he was performing the task and made a sacccade in that trial in an example session. The black and gray traces indicate the horizontal and vertical eye position respectively. In this session, the animal was required to perform a 15 visual angle degrees saccade to the upwards when he saw the fixation point jump. (recording session: tao-cueRF-edg-036-001+02).

Additional supplementary materials 2: Cells list

Note:
Depth: the zero point of the depth was the tip of the guide tube (ideally, it should be right under the dura).
Signal: If the number isbetween 8 - 10, it was a well-isolated unit.
Sac ampl (visual degree): saccade amplitude, the required saccade amplitude the animals should made in a given experiment.
xCo and yCo (mm): the x y coordinates of the recording site.
RFx, RFy (visual degree): the x and y coordinates of the receptive field. Minus means left in x and up in y.
PreS in cell (visual degree per second): the preferred speed of the neuron.
PreS in exp (visual degree per second): the speed of the stimuli in the experiment
PD in cell (visual degree): the preferred motion direction of the neuron.
hits/class: the number of hits for each class, one or more classes could be one condition depending on the experiment design.
The blank cells mean the data was unavailable, or could be found in the data.

date	*filename*	*channel*	*eletrode #*	*xCo*	*yCo*	*depth*	*linear tune*	*signal*	*spiral tuning*	*Sac ampl*	*StiSize*	*SacDir*	*RFx*	*RFy*	*RFsize*	*PreS in cell*	*PreS in exp*	*PD in exp (degree)*	*PD in cell (degree)*	*hits/class*
130913	tao-cueFRF-edg-004-001+01	5a		-2	-1	13493								excluded, not sure if MT						
130916	tao-cueFRF-edg-005-001+01	4a	4	-2	-1,5	14431	good	9	0	15	80	left	10	-1,5	7	16	16	180	150-210	40
130916	tao-cueFRF-edg-005-001+01	1a	1	-2	-1,5	14402	good	8	0	15	80	left	10	-1,5	7	16	16	180	60-120	40
130916	tao-cueFRF-edg-005-001+01	3a	3	-2	-1,5	13893	not	8	0	15	80	left	10	-1,5			16	180		40
130916	tao-cueFRF-edg-005-001+01	5a	5	-2	-1,5	13811	not	8	0	15	80	left	10	-1,5			16	180		40
130917	tao-cueFRF-edg-006-001+01	3a	3	-3	-3	14200	good	8	0	15	80	down	10	-5	10	8-16	16	0	270-0	60
130917	tao-cueFRF-edg-006-001+02	4a	4	-3	-3	14622	good	8	0	20	80	left	10	-10		16	16	90	90	60
130918	tao-cueFRF-edg-007-001+01		1	-2,9	-4	13745								excluded, not sure if MT						
130918	tao-cueFRF-edg-007-001+01		4	-2,9	-4	13745								excluded, not sure if MT						
130918	tao-cueFRF-edg-007-001+01		1	-2,9	-4	11198								excluded, not sure if MT						
130919	tao-cueFRF-edg-008-001+01	4a	4	-2,4	-4	14753	good	8	0	20	80	left	5,5	-11		16	16	150	30-60	70
130919	tao-cueFRF-edg-008-001+01	4b	4	-2,4	-4	14753	not	8	0	20	80	left	5,5	-11		not	16	150	not	70
130919	tao-cueFRF-edg-008-001+01	3a	3	-2,4	-4	13482	good	8	0	20	80	left	5,5	-11		16	16	150	150-180	70
130919	tao-cueFRF-edg-008-001+01	3b	3	-2,4	-4	13482	good	8	0	20	80	left	5,5	-11		all	16	150	150-180	70
130919	tao-cueFRF-edg-008-001+02	3a	3	-2,4	-4	14452	good	9	0	20	80	left	5,5	-11		16	16	60	60	40
130919	tao-cueFRF-edg-008-001+02	3b	3	-2,4	-4	14452	good	8	0	20	80	left	5,5	-11		16	16	60	60	40
130920	tao-cueFRF-edg-009-001+01	4a	4	-2,5	-4,5	14214		8	0	20	80	left	10	-10			4	30		70
130923	tao-cueFRF-edg-010-001+01	5a	5	-2	-4	13629	good	9	0	20	80	left	7	-11		all	4	150	120-180	80
130923	tao-cueFRF-edg-010-001+01	5b	5	-2	-4	13629	not	8	0	20	80	left	7	-11			4	150		80
130923	tao-cueFRF-edg-010-001+01	3a	3	-2	-4	13307	bad	8	0	20	80	left	7	-11			4	150		80
130923	tao-cueFRF-edg-010-001+01	3b	3	-2	-4	13307		8	0	20	80	left	7	-11			4	150		80
130924	tao-cueFRF-edg-011-001+01	1a	1	-3	-5	14600	not	8	0	20	80	left	6	-9			4	150		60

130924	tao-cueFRF-edg-011-001+01	5a	5	-3	-5	14100	good	8	0	20	80	left	6	-9		8-16	4	150	60-90	60
130924	tao-cueFRF-edg-011-001+01	4a	4	-3	-5	13800	not	8	0	20	80	left	6	-9			4	150		60
130924	tao-cueFRF-edg-011-001+02	5a	5	-3	-5	14000	good	8	0	20	80	left	6	-9		8-16	16	60	60-90	40
130925	tao-cueFRF-edg-012-001+01		3	-4	-3	14820								excluded, not sure if MT						
130926	tao-cueFRF-edg-013-001+01	2a	2	-2	-6,8	13206	good	8	0	20	80	left	8	8,5	10	16	16	60	30??	70
130926	tao-cueFRF-edg-013-001+01	1b	1	-2	-6,8	12726	good	8	0	20	80	left	8	8,5	10	16	16	60	300-330	70
130926	tao-cueFRF-edg-013-001+01	4a	4	-2	-6,8	12676	good	7	0	20	80	left	8	8,5	10	8-16	16	60	330	70
130926	tao-cueFRF-edg-013-001+01	3a	3	-2	-6,8	11582	good	8	0	20	80	left	8	8,5	10	8-16	16	60	30-90	70
130926	tao-cueFRF-edg-013-001+01	3b	3	-2	-6,8	11582	good	8	0	20	80	left	8	8,5	10	8-16	16	60	30-90	70
130926	tao-cueFRF-edg-013-001+01	5b	5	-2	-6,8	11398	good	7	0	20	80	left	8	8,5	10	8-16	16	60	30-60	70
130926	tao-cueFRF-edg-013-001+02	1a	1	-2	-6,8	12726	good	8	0	20	80	left	9	8,5		16	16	330	30	60
130926	tao-cueFRF-edg-013-001+02	1b	1	-2	-6,8	12726		8	0	20	80	left	9	8,5			16	330		60
130926	tao-cueFRF-edg-013-001+02	5a	5	-2	-6,8	11424		8	0	20	80	left	9	8,5			16	330		60
130926	tao-cueFRF-edg-013-001+02	5b	5	-2	-6,8	11424	good	8	0	20	80	left	9	8,5		16	16	330	300-0	60
130927	tao-cueFRF-edg-014-001+02	2a	2	-1,5	-6,5	13407	good	8	0	20	80	left	4	8		16	16	270	270-330	50
131001	tao-cueFRF-edg-016-001+01	3a	3	-1,8	-7	13034	good	9	0	20	80	left	10	13	10	16	16	90	60-120	70
131001	tao-cueFRF-edg-016-001+01	3b	3	-1,8	-7	13034	good	8	0	20	80	left	10	13	10	16	16	90	60-120	70
131001	tao-cueFRF-edg-016-001+02	3a	3	-1,8	-7	12095	good	8	0	20	80	left	8	13	10	16	16	90	90-120	70
131002	tao-cueFRF-edg-017-001+01	1a	1	-2,2	-6	15924	good	8	0	20	80	left	8	-8	8	16	16	0	300-0	70
131002	tao-cueFRF-edg-017-001+02	1a	1	-2,2	-6	15516	good	8	0	20	80	left	8	-8		16	16	0	210-330	55
131003	tao-cueFRF-edg-018-001+01	4a	4	-2,5	-5,5	16252	good	8	0	20	80	up	10	2	7	4	16	300	60	70
131003	tao-cueFRF-edg-018-001+01	4b	4	-2,5	-5,5	16252	good	8	0	20	80	up	10	2	7	16	16	300	300	70
131003	tao-cueFRF-edg-018-001+01	2b	2	-2,5	-5,5	15898	good	8	0	20	80	up	10	2		16	16	300	300	70
131003	tao-cueFRF-edg-018-001+01	3a	3	-2,5	-5,5	15520	tuned	8	0	20	80	up	10	2		16	16	300	300	70
131003	tao-cueFRF-edg-018-001+02	4a	4	-2,5	-5,5	15734		8	0	20	80	up	10	3			8	120		60
131003	tao-cueFRF-edg-018-001+02	3b	3	-2,5	-5,5	15520		8	0	20	80	up	10	3			8	120		60
131003	tao-cueFRF-edg-018-001+02	2a	2	-2,5	-5,5	15193	good	8	0	20	80	up	10	3		4-8	8	120	60-120	60
131004	tao-cueFRF-edg-019-001+01	2b	2	-1,8	-7	13083	good	8	0	20	80	left	6	11		8	8	120	120-150	60
131004	tao-cueFRF-edg-019-001+02	1b	1	-1,8	-7	13337	tuned	8	0	20	80	left	6	11		4	8	120	180	60
131004	tao-cueFRF-edg-019-001+02	2a	2	-1,8	-7	12843	tuned	8	0	20	80	left	6	11		16	8	120	180	60
131007	tao-cueFRF-edg-020-001+01		2	-3	-6	14082		8						excluded, not sure if MT						
131007	tao-cueFRF-edg-020-001+01		2	-3	-6	14082		8						excluded, not sure if MT						
131008	tao-cueFRF-edg-021-001+01	5a	5	-3	-4	15420	good	8	0	20	80	left	5,5	9	7	4-8	8	180	180-210	60
131009	tao-cueFRF-edg-022-001+01	4a	4	-4	-4	16252	tuned	8	0	20	80	left	4	-7,5	7	4	16	0	30-60	60
131009	tao-cueFRF-edg-022-001+01	4b	4	-4	-4	16252	not	8	0	20	80	left	4	-7,5	7		16	0		60
131009	tao-cueFRF-edg-022-001+01	2a	2	-4	-4	15776	tuned	8	0	20	80	left	4	-7,5	7	16	16	0	330-0	60
131009	tao-cueFRF-edg-022-001+01	2b	2	-4	-4	15776	good	8	0	20	80	left	4	-7,5	7	16	16	0	330-30	60
131011	tao-cueFRF-edg-024-001+01	3a	3	-3,5	-4	15637	not	8	0	15	80	down	9	-3			16	90		60
131011	tao-cueFRF-edg-024-001+01	3b	3	-3,5	-4	15637	not	8	0	15	80	down	9	-3			16	90		60
131011	tao-cueFRF-edg-024-001+01	4a	4	-3,5	-4	14043	good	8	0	15	80	down	9	-3		16	16	90	90	60

131014	tao-cueFRF-edg-025-001+01	3a	3	-3	-3,5	15637	tuned	8	0	20	80	left	2	-9	8	16	210	210	60
131014	tao-cueFRF-edg-025-001+01	3b	3	-3	-3,5	15637	good	8	0	20	80	left	2	-9	8-16	16	210	180-240	60
131014	tao-cueFRF-edg-025-001+01	1a	1	-3	-3,5	15397	not	8	0	20	80	left	2	-9		16	210		60
131014	tao-cueFRF-edg-025-001+01	2a	2	-3	-3,5	14746	tuned	8	0	20	80	left	2	-9	16	16	210	120	60
131015	tao-cueFRF-edg-026-001+01	2a	2	-4	-5	13520	good	8	0	10	80	up	5	1	4	4	60	60	70
131016	tao-cueFRF-edg-027-001+01	1a	1	-3	-3	14700	good	8	0	15	80	up	6,5	1	16	16	90	30-90	70
131016	tao-cueFRF-edg-027-001+01	5b	5	-3	-3	14572	not		0	15	80	up	6,5	1		16	90		70
131016	tao-cueFRF-edg-027-001+01	2b	2	-3	-3	14383	not	8	0	15	80	up	6,5	1		16	90		70
131016	tao-cueFRF-edg-027-001+02	5a	5	-3	-3	14572	good		0	15	80	up	6,5	1	16	16	270	270	60
131205	tao-cueFRF-edg-037-001+01		4	-0,8	-6,8	10880	excluded, unusable because experimental parameters were different from other recording session												
131205	tao-cueFRF-edg-037-001+02		4	-0,8	-6,8	10780	excluded, unusable because experimental parameters were different from other recording session												
140604	tao-cueFRF-edg-071-001+01		2	-1,5	-6	9935	excluded, unusable because experimental parameters were different from other recording session												
140604	tao-cueFRF-edg-071-001+02		2	-1,5	-6	9935	excluded, unusable because experimental parameters were different from other recording session												
140604	tao-cueFRF-edg-071-001+03		3	-1,5	-6	9378	excluded, unusable because experimental parameters were different from other recording session												
130923	tao-cueRF-edg-010-001+01	5a	5	-2	-4	13629	exluded because the monkeyes was not yet fully trianed on this task												
130924	tao-cueRF-edg-011-001+01	5a	5	-3	-5	14100	exluded because the monkeyes was not yet fully trianed on this task												
130926	tao-cueRF-edg-013-001+01	5a	5	-2	-6,8	11582	exluded because the monkeyes was not yet fully trianed on this task												
130926	tao-cueRF-edg-013-001+01	5b	5	-2	-6,8	11398	exluded because the monkeyes was not yet fully trianed on this task												
130926	tao-cueRF-edg-013-001+01	3b	3	-2	-6,8	11347	exluded because the monkeyes was not yet fully trianed on this task												
131001	tao-cueRF-edg-016-001+01	3a	3	-1,8	-7	13034	exluded because the monkeyes was not yet fully trianed on this task												
131002	tao-cueRF-edg-017-001+01	1a	1	-2,2	-6	15924	exluded because the monkeyes was not yet fully trianed on this task												
131008	tao-cueRF-edg-021-001+01	5a	5	-3	-4	15420	exluded because the monkeyes was not yet fully trianed on this task												
131009	tao-cueRF-edg-022-001+01	4a	4	-4	-4	15520	exluded because the monkeyes was not yet fully trianed on this task												
131010	tao-cueRF-edg-023-001+01	3b	3	-4,5	-4	15235	exluded because the monkeyes was not yet fully trianed on this task												
131011	tao-cueRF-edg-024-001+01	4a	4	-3,5	-4	14043	exluded because the monkeyes was not yet fully trianed on this task												
131014	tao-cueRF-edg-025-001+01	3b	3	-3	-3,5	15637	exluded because the monkeyes was not yet fully trianed on this task												
131015	tao-cueRF-edg-026-001+01	2a	2	-4	-5	13520	exluded because the monkeyes was not yet fully trianed on this task												
131016	tao-cueRF-edg-027-001+01	1a	1	-3	-3	14700	exluded because the monkeyes was not yet fully trianed on this task												
131121	tao-cueRF-edg-028-001+01	1a	1	-2	-5	14453	good	8	0	15	80	right	3	-9	8	8	180	180-210	60
131121	tao-cueRF-edg-028-001+01	1b	1	-2	-5	14453	tuned	8	0	15	80	right	3	-9	8-16	8	180	270	60
131121	tao-cueRF-edg-028-001+02	1a	1	-2	-5	14064	good	8	0	15	80	right	3	-7	4-8	4	270	330	55
131121	tao-cueRF-edg-028-001+02	1b	1	-2	-5	14064	good	7	0	15	80	right	3	-7	4-8	4	270	270-300	55
131122	tao-cueRF-edg-029-001+01	4b	4	-2	-7	9575	good	8	0	15	80	right	3	7	16	16	180	240	30
131126	tao-cueRF-edg-030-001+01	4a	4	-1	-7	9780	good	8	0	15	80	right	6	9	16	16	270	240-270	60
131126	tao-cueRF-edg-030-001+01	4b	4	-1	-7	9780	good	8	0	15	80	right	6	9	16	16	270	210-270	60
131126	tao-cueRF-edg-030-001+01	3b	3	-1	-7	9556	tuned	8	0	15	80	right	6	9	4-8	16	270	210-240	60
131126	tao-cueRF-edg-030-001+01	3a	3	-1	-7	9556	good	8	0	15	80	right	6	9	16	16	270	210-240	60
131126	tao-cueRF-edg-030-001+01	1a	1	-1	-7	9442	good	8	0	15	80	right	6	9	4	16	270	240	60
131126	tao-cueRF-edg-030-001+02	4a	4	-1	-7	9549	good	8	0	15	80	right	6	9	16	16	330	300-330	55
131126	tao-cueRF-edg-030-001+02	3a	3	-1	-7	9047	not	8	0	15	80	right	6	9		16	330		55

131127	tao-cueRF-edg-031-001+01	5a	5	-0,5	-7	8523	good	8	0	15	80	right	10	11		16	16	90	60-120	55
131128	tao-cueRF-edg-032-001+01	1a	1	-0,5	-6	10380	good	8	0	15	80	right	7	8	10	16	16	60	30-90	50
131128	tao-cueRF-edg-032-001+01	1b	1	-0,5	-6	10380	good	8	0	15	80	right	7	8		16	16	60	60	50
131129	tao-cueRF-edg-033-001+01	4a	4	-1	-6,5	10288	good	8	0	15	80	right	9	10	10	16	16	180	180	50
131129	tao-cueRF-edg-033-001+01	4b	4	-1	-6,5	10288	good	8	0	15	80	right	9	10	10	16	16	180	180	50
131129	tao-cueRF-edg-033-001+02	4a	4	-1	-6,5	10412		8	0	15	80	right	9	10	10		16	270		50
131129	tao-cueRF-edg-033-001+02	4b	4	-1	-6,5	10412	good	8	0	15	80	right	9	10	10	8-16	16	270	270	50
131129	tao-cueRF-edg-033-001+03	5a	5	-1	-6,5	8741	good	8	0	15	80	right	11	10	15	all	16	180	180-240	50
131129	tao-cueRF-edg-033-001+03	5b	5	-1	-6,5	8741	good	8	0	15	80	right	11	10	15	16	16	180	270	50
131203	tao-cueRF-edg-035-001+01	5a	4	-0,8	-6,6	10705	good	8	0	15	80	right	9	9		16	16	0	270-330	60
131203	tao-cueRF-edg-035-001+01	3b	5	-0,8	-6,6	10674	good	8	0	15	80	right	9	9		8-16	16	0	330-0	60
131203	tao-cueRF-edg-035-001+01	5b	5	-0,8	-6,6	10674	good	8	0	15	80	right	9	9		all	16	0	330-0	60
131203	tao-cueRF-edg-035-001+01	4a	3	-0,8	-6,6	10553	good	8	0	15	80	right	9	9		8	16	0	90	60
131203	tao-cueRF-edg-035-001+02	4a	3	-0,8	-6,6	10553	good	8	0	15	80	down	9	3		16	16	90	90	60
131203	tao-cueRF-edg-035-001+02	5a	4	-0,8	-6,6	10538	good	8	0	15	80	down	9	3		16	16	90	330	60
131203	tao-cueRF-edg-035-001+02	3b	5	-0,8	-6,6	10538		8	0	15	80	down	9				16	90	??	60
131204	tao-cueRF-edg-036-001+01		4	-0,5	-6,8	10888								excluded, same neurons as in +02						
131204	tao-cueRF-edg-036-001+01		4	-0,5	-6,8	10888								excluded, same neurons as in +02						
131204	tao-cueRF-edg-036-001+01		3	-0,5	-6,8	10621								excluded, same neurons as in +02						
131204	tao-cueRF-edg-036-001+02	4a	4	-0,5	-6,8	10888	good	8	0	15	80	up	11	0		16	16	180	180	50
131204	tao-cueRF-edg-036-001+02	4b	4	-0,5	-6,8	10888	good	8	0	15	80	up	11	0		16	16	180	180	50
131204	tao-cueRF-edg-036-001+02	3a	3	-0,5	-6,8	10621	good	8	0	15	80	up	11	0		16	16	180	210-240	50
131204	tao-cueRF-edg-036-001+03	3b	5	-0,5	-6,8	10968	tuned	8	0	15	80	up	11	0		16	16	60	0-30	25
131204	tao-cueRF-edg-036-001+03	5a	3	-0,5	-6,8	10621	good	8	0	15	80	up	11	0		16	16	60	60	25
131204	tao-cueRF-edg-036-001+04	3a	3	-0,5	-6,8	10968		8	0	15	80	up	11	0			16	210		55
131204	tao-cueRF-edg-036-001+04	5a	4	-0,5	-6,8	10968		8	0	15	80	up	11	0			16	210		55
131204	tao-cueRF-edg-036-001+04	4a	4	-0,5	-6,8	10968		8	0	15	80	up	11	0			16	210		55
131204	tao-cueRF-edg-036-001+04	4b	5	-0,5	-6,8	10968		8	0	15	80	up	11	0			16	210		55
131205	tao-cueRF-edg-037-001+01	2a	2	-0,8	-6,8	11689	good	8	0	15	80	up	10	0,5		16	16	300	300	45
131205	tao-cueRF-edg-037-001+02	4a	4	-0,8	-6,8	10880	good	8	0	15	80	up	10	0,5		16	16	150	150	50
131205	tao-cueRF-edg-037-001+02	4b	4	-0,8	-6,8	10880	good	8	0	15	80	up	10	0,5		16	16	150	120-150	50
131205	tao-cueRF-edg-037-001+02	3a	3	-0,8	-6,8	10280	not	8	0	15	80	up	10	0,5			16	150		50
131205	tao-cueRF-edg-037-001+03		4	-0,8	-6,8	10880		8						excluded, not enough trials						14--15
131205	tao-cueRF-edg-037-001+03		4	-0,8	-6,8	10880		8						excluded, not enough trials						14--15
131205	tao-cueRF-edg-037-001+04	5a	5	-0,8	-6,8	10500		8	0	15	80	up	10	0,5			16	210		50
131205	tao-cueRF-edg-037-001+04	5b	5	-0,8	-6,8	10500		8	0	15	80	up	10	0,5			16	210		50
130531	tao-cueFRF-hay-491-001+01	3a	3	-2,3	-1	11602	good	8	0	15	80	right	-1	-9	10	16	16	90	60-90	20

130531	tao-cueFRF-hay-491-001+01	5a	5	-2,3	-1	11675	good	8	0	15	80	right	-1	-9	10	8-16	16	90	60-120	20
130531	tao-cueFRF-hay-491-001+02	1a	1	-2,3	-1	10835		8	0	15	80	right	-1	-9			16	90		30
130531	tao-cueFRF-hay-491-001+02	1b	1	-2,3	-1	10835		8	0	15	80	right	-1	-9			16	90		30
130531	tao-cueFRF-hay-491-001+02	3a	3	-2,3	-1	11602	good	8	0	15	80	right	-1	-9			16	90		30
130531	tao-cueFRF-hay-491-001+02	3b	3	-2,3	-1	11602	good	8	0	15	80	right	-1	-9			16	90		30
130531	tao-cueFRF-hay-491-001+02	5a	5	-2,3	-1	11675	good	9	0	15	80	right	-1	-9			16	90		30
130531	tao-cueFRF-hay-491-001+02	5b	5	-2,3	-1	11675		8	0	15	80	right	-1	-9			16	90		30
130607	tao-cueFRF-hay-493-001+01	3a	3	-2,3	-1,5	11888	good	8	0	15	80	right	-2	-7,5		4	16	300	0	60
130607	tao-cueFRF-hay-493-001+01	4a	4	-2,3	-1,5	11730	good	8	0	15	80	right	-2	-7,5		8	16	300	30-60	60
130607	tao-cueFRF-hay-493-001+01	4b	4	-2,3	-1,5	11730	good	8	0	15	80	right	-2	-7,5		16	16	300	300	60
130611	tao-cueFRF-hay-495-001+01	1a	1	-3	-1	10605	good	8	0	15	80	right	-1	-8		all	16	90	90-120	60
130611	tao-cueFRF-hay-495-001+01	4a	4	-3	-1	11233	tuned	8	0	15	80	right	-1	-8		4	16	90	0	60
130611	tao-cueFRF-hay-495-001+01	5a	5	-3	-1	11093	good	8	0	15	80	right	-1	-8		all	16	90	300-330	60
130611	tao-cueFRF-hay-495-001+02	1a	1	-3	-1	11000	good	8	0	15	80	right	-1	-8		16	16	90	90-120	70
130611	tao-cueFRF-hay-495-001+02	1b	1	-3	-1	11000	good	8	0	15	80	right	-1	-8		all	16	90	90	70
130611	tao-cueFRF-hay-495-001+02	4a	4	-3	-1	11310	good	8	0	15	80	right	-1	-8		16	16	90	90	70
130611	tao-cueFRF-hay-495-001+02	4b	4	-3	-1	11310	good	8	0	15	80	right	-1	-8		16	16	90	60-120	70
130613	tao-cueFRF-hay-496-001+01	1a	1	-2,8	-1,3	10503	good	9	0	15	80	right	-3,5	-7,5		4-8	8	270	240-300	60
130613	tao-cueFRF-hay-496-001+01	3a	3	-2,8	-1,3	10538	good	8	0	15	80	right	-3,5	-7,5		4-8	8	270	300-0	60
130613	tao-cueFRF-hay-496-001+01	3b	3	-2,8	-1,3	10538	good	8	0	15	80	right	-3,5	-7,5		4-8	8	270	30-90	60
130613	tao-cueFRF-hay-496-001+01	5a	5	-2,8	-1,3	10448	good	8	0	15	80	right	-3,5	-7,5		8-16	8	270	240-300	60
130613	tao-cueFRF-hay-496-001+01	5b	5	-2,8	-1,3	10448	good	8	0	15	80	right	-3,5	-7,5		8-16	8	270	210-270	60
130614	tao-cueFRF-hay-497-001+01	1a	1	-2,8	-1,3	11137	good	8	0	15	80	right	-1,5	-9,5		16	16	30	30-60	40
130614	tao-cueFRF-hay-497-001+01	5a	5	-2,8	-1,3	11100	tuned	8	0	15	80	right	-1,5	-9,5		16	16	30	240	40
130614	tao-cueFRF-hay-497-001+01	5b	5	-2,8	-1,3	11100	good	8	0	15	80	right	-1,5	-9,5		16	16	30	240	40
130620	tao-cueFRF-hay-500-001+01	2a	2	-2,8	-1,3	11845	good	8	0	15	80	right	-3	-10		16	4	0	60-120	60
130620	tao-cueFRF-hay-500-001+01	3a	3	-2,8	-1,3	11115	good	8	0	15	80	right	-3	-10		4-8	4	0	330-0	60
130620	tao-cueFRF-hay-500-001+01	3b	3	-2,8	-1,3	11115	good	8	0	15	80	right	-3	-10		4-8	4	0	330-0	60
130622	tao-cueFRF-hay-502-001+01	1a	1	-2,7	-1,4	10868	good	8	0	15	80	right	-3	-10		8	8	330	240-0	30
130622	tao-cueFRF-hay-502-001+01	1b	1	-2,7	-1,4	10868	good	8	0	15	80	right	-3	-10		8	8	330	300	30
130622	tao-cueFRF-hay-502-001+01	3a	3	-2,7	-1,4	11115	good	8	0	15	80	right	-3	-10		4-8	8	330	270-330	30
130623	tao-cueFRF-hay-503-001+01	2a	2	-2,8	-1,3	11500	good	8	0	15	80	right	-3,5	-10		4	4	300	300-330	40
130623	tao-cueFRF-hay-503-001+01	2b	2	-2,8	-1,3	11500	good	8	0	15	80	right	-3,5	-10		all	4	300	270-330	40
130623	tao-cueFRF-hay-503-001+01	3b	3	-2,8	-1,3	11010	tuned	8	0	15	80	right	-3,5	-10		4-8	4	300	330	40
130625	tao-cueFRF-hay-504-001+01	1a	1	-2,8	-1,3	11143	good	8	0	15	80	right	-2,5	-10		16	16	0	0-30	60
130625	tao-cueFRF-hay-504-001+01	1b	1	-2,8	-1,3	11143	good	7	0	15	80	right	-2,5	-10		16	16	0	0	60
130625	tao-cueFRF-hay-504-001+01	2a	2	-2,8	-1,3	11680	good	9	0	15	80	right	-2,5	-10		8-16	16	0	0	60
130625	tao-cueFRF-hay-504-001+01	3a	3	-2,8	-1,3	11236	good	8	0	15	80	right	-2,5	-10		4-8	16	0	270-330	60
130625	tao-cueFRF-hay-504-001+01	3b	3	-2,8	-1,3	11236	not	7	0	15	80	right	-2,5	-10			16	0	all	60
130809	tao-cueFRF-hay-506-001+01	1a	1	-2,6	-1,2	10695	good	9	0	15	80	right	-2,5	-10		16	16	180	180	60

130809	tao-cueFRF-hay-506-001+01	1b	1	-2,6	-1,2	10695	good	8	0	15	80	right	-2,5	-10	16	16	180	120	60
130809	tao-cueFRF-hay-506-001+01	4a	4	-2,6	-1,2	11044	good	8	0	15	80	right	-2,5	-10	8-16	16	180	150-210	60
130809	tao-cueFRF-hay-506-001+01	5a	5	-2,6	-1,2	10639	good	8	0	15	80	right	-2,5	-10	16	16	180	0	60
130809	tao-cueFRF-hay-506-001+01	5b	5	-2,6	-1,2	10639	good	8	0	15	80	right	-2,5	-10	16	16	180	0	60
130816	tao-cueFRF-hay-507-001+01	3a	3	-2,6	-1,2	10903	good	8	0	15	80	right	-2,5	-10	8-16	16	180	180	70
130816	tao-cueFRF-hay-507-001+01	3b	3	-2,6	-1,2	10903	good	8	0	15	80	right	-2,5	-10	all	16	180	180-210	70
130816	tao-cueFRF-hay-507-001+01	4a	4	-2,6	-1,2	11508	good	8	0	15	80	right	-2,5	-10	all	16	180	30-90	70
130822	tao-cueFRF-hay-508-001+01	1a	1	-2,6	-1,2	10673	good	8	0	15	80	right	-7	-10	16	16	90	60-120	70
130822	tao-cueFRF-hay-508-001+01	1b	1	-2,6	-1,2	10673	good	8	0	15	80	right	-7	-10	8-16	16	90	60-120	70
130822	tao-cueFRF-hay-508-001+01	3a	3	-2,6	-1,2	10640		8	0	15	80	right	-7	-10		16	90		70
130822	tao-cueFRF-hay-508-001+01	3b	3	-2,6	-1,2	10640		8	0	15	80	right	-7	-10		16	90		70
130822	tao-cueFRF-hay-508-001+01	5a	5	-2,6	-1,2	10911	good	9	0	15	80	right	-7	-10	16	16	90	90-120	70
130822	tao-cueFRF-hay-508-001+01	5b	5	-2,6	-1,2	10911	good	9	0	15	80	right	-7	-10	16	16	90	90-120	70
130828	tao-cueFRF-hay-509-001+01	3a	3	-2,6	-1,2	10200	good	8	0	15	80	right	-5	-10	8	16	90	300	60
130828	tao-cueFRF-hay-509-001+01	4a	4	-2,6	-1,2	10200	good	9	0	15	80	right	-5	-10	16	16	90	90-120	60
130828	tao-cueFRF-hay-509-001+02	1a	1	-2,6	-1,2	10664	tuned	8	0	15	80	right	-5	-10	all	16	270	90-180	60
130828	tao-cueFRF-hay-509-001+02	3a	3	-2,6	-1,2	10427	tuned	8	0	15	80	right	-5	-10	8-16	16	270	330	60
130828	tao-cueFRF-hay-509-001+02	3b	3	-2,6	-1,2	10427	good	9	0	15	80	right	-5	-10	16	16	270	240-300	60
130828	tao-cueFRF-hay-509-001+02	4a	4	-2,6	-1,2	10995	good	8	0	15	80	right	-5	-10	16	16	270	90-120	60
130829	tao-cueFRF-hay-510-001+01	1a	1	-2,5	-1,1	10374	good	8	0	15	80	right	-4	-12	16	16	240	240	45
130829	tao-cueFRF-hay-510-001+01	1b	1	-2,5	-1,1	10374	good	8	0	15	80	right	-4	-12	16	16	240	210-270	45
130829	tao-cueFRF-hay-510-001+02	4a	4	-2,5	-1,1	10427	good	9	0	15	80	right	-4	-12	16	16	0	330-0	55
130829	tao-cueFRF-hay-510-001+02	4b	4	-2,5	-1,1	10427	good	8	0	15	80	right	-4	-12	all	16	0	120-180	55
130830	tao-cueFRF-hay-511-001+01	1a	1	-2,3	-1,3	10321	good	8	0	15	80	right	-3	-12	16	16	240	180-240	60
130830	tao-cueFRF-hay-511-001+01	3a	3	-2,3	-1,3	10533	not	8	0	15	80	right	-3	-12		16	240		60
130830	tao-cueFRF-hay-511-001+01	5a	5	-2,3	-1,3	10203	not	8	0	15	80	right	-3	-12		16	240		60
130904	tao-cueFRF-hay-512-001+01	3a	3	-2,6	-1,3	10530	good	8	0	20	80	right	-5	-11	16	16	0	330-0	70
130904	tao-cueFRF-hay-512-001+01	3b	3	-2,6	-1,3	10530	good	8	0	20	80	right	-5	-11	all	16	0	90	70
130905	tao-cueFRF-hay-513-001+01	1a	1	-2,5	-1	10260	good	8	0	20	80	right	-5	-13	16	16	270	270-300	70
130905	tao-cueFRF-hay-513-001+02	3a	3	-2,5	-1	10347	good	8	0	20	80	right	-5	-13	all	16	180	150-210	50
130906	tao-cueFRF-hay-514-001+01	1a	1	-2,7	-1,2	10227	good	8	0	20	80	right	-5	-13	16	16	240	240-300	70
130906	tao-cueFRF-hay-514-001+01	1b	1	-2,7	-1,2	10227	tuned	8	0	20	80	right	-5	-13	16	16	240		70
130607	tao-cueRF-hay-493-001+01	4b	4	-2,3	-1,5	11730	good	8	0	15	80	left	-2	-7,5	16	16	300	300	60
130611	tao-cueRF-hay-495-001+01	1a	1	-3	-1	10605	good	8	0	15	80	left	-1	-8	16	16	90	90-120	60
130611	tao-cueRF-hay-495-001+01	1b	1	-3	-1	11000	good	8	0	15	80	left	-1	-8	all	16	90	90	60
130611	tao-cueRF-hay-495-001+01	4a	4	-3	-1	11310	not	8	0	15	80	left	-1	-8	4	16	90	0-60	60
130611	tao-cueRF-hay-495-001+01	4b	4	-3	-1	11310	good	7	0	15	80	left	-1	-8	16	16	90	60-120	60
130611	tao-cueRF-hay-495-001+01	5a	5	-3	-1	11093	good	8	0	15	80	left	-1	-8	16	16	90	300-330	60
130613	tao-cueRF-hay-496-001+01	1b	1	-2,8	-1,3	10503	not	8	0	15	80	left	-3,5	-7,5		8	270		60
130613	tao-cueRF-hay-496-001+02	1a	1	-2,8	-1,3	10503							excluded,not enough trials						4--5

130613	tao-cueRF-hay-496-001+02	5a	5	-2,8	-1,3	10448	good	8	0	15	80	left	-3,5	-7,5	8-16	8	270	240-300	60
130613	tao-cueRF-hay-496-001+02	5b	5	-2,8	-1,3	10448	good	8	0	15	80	left	-3,5	-7,5	8-16	8	270	210-270	60
130614	tao-cueRF-hay-497-001+01	1a	1	-2,8	-1,3	11100	excluded,not enough trials												14--15
130614	tao-cueRF-hay-497-001+02	1a	1	-2,8	-1,3	11137	good	7	0	15	80	right	-1,5	-9,5	16	16	30	30-60	40
130614	tao-cueRF-hay-497-001+02	1b	1	-2,8	-1,3	11137	good	8	0	15	80	right	-1,5	-9,5	16	16	30	0-60	40
130614	tao-cueRF-hay-497-001+02	4a	4	-2,8	-1,3	11285	tuned	8	0	15	80	right	-1,5	-9,5	16	16	30	60	40
130614	tao-cueRF-hay-497-001+02	5a	5	-2,8	-1,3	11100	good	9	0	15	80	right	-1,5	-9,5	16	16	30	240	40
130614	tao-cueRF-hay-497-001+02	5b	5	-2,8	-1,3	11100	good	8	0	15	80	right	-1,5	-9,5	16	16	30	240	40
130618	tao-cueRF-hay-498-001+01	5a	5	-2,8	-1,3	10740	good	8	0	15	80	left	-3	-10	all	8	300	300-330	50
130618	tao-cueRF-hay-498-001+01	5b	5	-2,8	-1,3	10740	good	7	0	15	80	left	-3	-10	all	8	300	270-330	50
130619	tao-cueRF-hay-499-001+01	1a	1	-2,8	-1,3	11580	good	9	0	15	80	left	-2,5	-10	8-16	8	180	180-210	40
130619	tao-cueRF-hay-499-001+01	1b	1	-2,8	-1,3	11580	good	8	0	15	80	left	-2,5	-10	4-8	8	180	150	40
130619	tao-cueRF-hay-499-001+01	2a	2	-2,8	-1,3	11880	good	8	0	15	80	left	-2,5	-10	all	8	180	300-330	40
130619	tao-cueRF-hay-499-001+01	3b	3	-2,8	-1,3	11280	good	8	0	15	80	left	-2,5	-10	8	8	180	150-210	40
130619	tao-cueRF-hay-499-001+01	5a	5	-2,8	-1,3	11570	good	8	0	15	80	left	-2,5	-10	all	8	180	0	40
130620	tao-cueRF-hay-500-001+01	1a	1	-2,8	-1,3	11218	good	8	0	15	80	left	-3	-10	4	4	0	120-210	60
130620	tao-cueRF-hay-500-001+01	2a	2	-2,8	-1,3	11845	good	8	0	15	80	left	-3	-10	16	4	0	60-120	60
130620	tao-cueRF-hay-500-001+01	3a	3	-2,8	-1,3	11115	good	8	0	15	80	left	-3	-10	4-8	4	0	330-0	60
130620	tao-cueRF-hay-500-001+01	3b	3	-2,8	-1,3	11115	good	8	0	15	80	left	-3	-10	4-8	4	0	330-0	60
130620	tao-cueRF-hay-500-001+02	3b	3	-2,8	-1,3	11115	excluded,not enough trials												10
130622	tao-cueRF-hay-502-001+01	1a	1	-2,7	-1,4	10868	good	8	0	15	80	left	-3	-10	8	8	330	240-0	25
130622	tao-cueRF-hay-502-001+01	1b	1	-2,7	-1,4	10868	good	7	0	15	80	left	-3	-10	8	8	330	300	25
130622	tao-cueRF-hay-502-001+01	3a	3	-2,7	-1,4	11115	good	8	0	15	80	left	-3	-10	4-8	8	330	270-330	25
130623	tao-cueRF-hay-503-001+01	1a	1	-2,8	-1,3	10800	good	8	0	15	80	left	-3,5	-10	4	4	300	270-330	40
130623	tao-cueRF-hay-503-001+01	2a	2	-2,8	-1,3	11500	good	8	0	15	80	left	-3,5	-10	4	4	300	300-330	40
130623	tao-cueRF-hay-503-001+01	2b	2	-2,8	-1,3	11500	good	8	0	15	80	left	-3,5	-10	all	4	300	270-330	40
130623	tao-cueRF-hay-503-001+01	3a	3	-2,8	-1,3	11010	good	9	0	15	80	left	-3,5	-10	4	4	300	270-330	40
130625	tao-cueRF-hay-504-001+01	1a	1	-2,8	-1,3	11143	good	8	0	15	80	left	-2,5	-10	16	16	0	0-30	60
130625	tao-cueRF-hay-504-001+01	1b	1	-2,8	-1,3	11143	good	7	0	15	80	left	-2,5	-10	16	16	0	0	60
130625	tao-cueRF-hay-504-001+01	2a	2	-2,8	-1,3	11680	good	9	0	15	80	left	-2,5	-10	8-16	16	0	0	60
130625	tao-cueRF-hay-504-001+01	2b	2	-2,8	-1,3	11680	good	9	0	15	80	left	-2,5	-10	16	16	0	330-0	60
130625	tao-cueRF-hay-504-001+02	3a	3	-2,8	-1,3	11236	good	8	0	15	80	left	-2,5	-10	4-8	16	0	270-330	20
130808	tao-cueRF-hay-505-001+01	4a	4	-2,8	-1,3	11300	good	8	0	15	80	left	-2,5	-10	16	16	0	0	40
130808	tao-cueRF-hay-505-001+01	4b	4	-2,8	-1,3	11300	good	8	0	15	80	left	-2,5	-10		16	0	0	40
130808	tao-cueRF-hay-505-001+01	5a	5	-2,8	-1,3	10561	good	8	0	15	80	left	-2,5	-10	all	16	0	330-30	40
130808	tao-cueRF-hay-505-001+01	5b	5	-2,8	-1,3	10561	good	8	0	15	80	left	-2,5	-10	16	16	0	330-0	40
130808	tao-cueRF-hay-505-001+02	4a	4	-2,8	-1,3	11000	good	8	0	15	80	left	-2,5	-10	16	16	0	0	50
130808	tao-cueRF-hay-505-001+02	5a	5	-2,8	-1,3	10460	good	8	0	15	80	left	-2,5	-10	16	16	0	0	50
130808	tao-cueRF-hay-505-001+02	5b	5	-2,8	-1,3	10460	good	8	0	15	80	left	-2,5	-10	16	16	0	0	50
130808	tao-cueRF-hay-505-001+03	5a	5	-2,8	-1,3	10309	good	8	0	15	80	left	-2,5	-10	16	16	0	0	40

130808	tao-cueRF-hay-505-001+03	5b	5	-2,8	-1,3	10309	good	8	0	15	80	left	-2,5	-10	16	16	0	0	40
130809	tao-cueRF-hay-506-001+01	1a	1	-2,6	-1,2	10695	good	9	0	15	80	left	-2,5	-10	16	16	180	180	50
130809	tao-cueRF-hay-506-001+01	5a	5	-2,6	-1,2	10639	good	7	0	15	80	left	-2,5	-10	16	16	180	0	50
130809	tao-cueRF-hay-506-001+01	5b	5	-2,6	-1,2	10639	good	9	0	15	80	left	-2,5	-10	16	16	180	0	50
130809	tao-cueRF-hay-506-001+02	1b	1	-2,6	-1,2	10715	good	8	0	15	80	left	-2,5	-10	8-16	16	180	180	70
130809	tao-cueRF-hay-506-001+02	4a	4	-2,6	-1,2	11454	good	9	0	15	80	left	-2,5	-10	16	16	180	150-210	70
130816	tao-cueRF-hay-507-001+01	1a	1	-2,6	-1,2	10803	good	8	0	15	80	left	-2,5	-10	16	16	180	240	60
130816	tao-cueRF-hay-507-001+01	3a	3	-2,6	-1,2	10803	good	8	0	15	80	left	-2,5	-10	8-16	16	180	180	60
130816	tao-cueRF-hay-507-001+01	3b	3	-2,6	-1,2	10803	good	8	0	15	80	left	-2,5	-10	all	16	180	180-210	60
130816	tao-cueRF-hay-507-001+01	4a	4	-2,6	-1,2	11508	good	8	0	15	80	left	-2,5	-10	all	16	180	30-90	60
130816	tao-cueRF-hay-507-001+01	5a	5	-2,6	-1,2	10808	tuned	8	0	15	80	left	-2,5	-10	16	16	180	90-330	60
130816	tao-cueRF-hay-507-001+02	3a	3	-2,6	-1,2	10903	good	8	0	15	80	left	-2,5	-10	8-16	16	180	180	40
130816	tao-cueRF-hay-507-001+02	3b	3	-2,6	-1,2	10903	good	8	0	15	80	left	-2,5	-10	all	16	180	180-210	40
130816	tao-cueRF-hay-507-001+02	4a	4	-2,6	-1,2	11508	good	8	0	15	80	left	-2,5	-10	all	16	180	30-90	40
130816	tao-cueRF-hay-507-001+02	5a	5	-2,6	-1,2	10808	tuned	8	0	15	80	left	-2,5	-10	16	16	180	90-330	40
130816	tao-cueRF-hay-507-001+03	1b	1	-2,6	-1,2	10758	good	8	0	15	80	left	-2,5	-10	16	16	180	180-240	35
130816	tao-cueRF-hay-507-001+03	4a	4	-2,6	-1,2	11384	good	8	0	15	80	left	-2,5	-10	all	16	180	30-90	35
130822	tao-cueRF-hay-508-001+01	1a	1	-2,6	-1,2	10673	good	8	0	15	80	left	-7	-10	16	16	90	60-120	40
130822	tao-cueRF-hay-508-001+01	1b	1	-2,6	-1,2	10673	good	8	0	15	80	left	-7	-10	8-16	16	90	60-120	40
130822	tao-cueRF-hay-508-001+01	3a	3	-2,6	-1,2	10640	not	8	0	15	80	left	-7	-10		16	90	60-120	40
130822	tao-cueRF-hay-508-001+01	3b	3	-2,6	-1,2	10640	not	8	0	15	80	left	-7	-10		16	90		40
130822	tao-cueRF-hay-508-001+01	5a	5	-2,6	-1,2	10911	good	9	0	15	80	left	-7	-10	16	16	90	90-120	40
130822	tao-cueRF-hay-508-001+01	5b	5	-2,6	-1,2	10911	good	9	0	15	80	left	-7	-10	16	16	90	90-120	40
130828	tao-cueRF-hay-509-001+01		1	-2,6	-1,2	10995							excluded,not enough trials						7--8
130828	tao-cueRF-hay-509-001+01		3	-2,6	-1,2	10200							excluded,not enough trials						7--8
130829	tao-cueRF-hay-510-001+01	1a	1	-2,5	-1,1	10374	good	8	0	15	80	left	-4	-12	16	16	0	180-300	40
130829	tao-cueRF-hay-510-001+01	1b	1	-2,5	-1,1	10374	good	7	0	15	80	left	-4	-12	16	16	0	210-270	40
130829	tao-cueRF-hay-510-001+01	4a	4	-2,5	-1,1	10427	good	9	0	15	80	left	-4	-12	16	16	0	330-0	40
130829	tao-cueRF-hay-510-001+01	4b	4	-2,5	-1,1	10427	good	8	0	15	80	left	-4	-12	all	16	0	120-180	40
130830	tao-cueRF-hay-511-001+01	1a	1	-2,3	-1,3	10321	good	8	0	15	80	left	-3	-12	16	16	240	180-240	45
130830	tao-cueRF-hay-511-001+01	3a	3	-2,3	-1,3	10533	not	8	0	15	80	left	-3	-12		16	240		45
130904	tao-cueRF-hay-512-001+01	3a	3	-2,6	-1,3	10530	good	8	0	20	80	left	-5	-11	16	16	0	330-0	60
130904	tao-cueRF-hay-512-001+01	3b	3	-2,6	-1,3	10530	good	8	0	20	80	left	-5	-11	all	16	0	90	60
130905	tao-cueRF-hay-513-001+01	1a	1	-2,5	-1	10260	good	8	0	20	80	left	-5	-13	16	16	270	270-300	50
130905	tao-cueRF-hay-513-001+01	3a	3	-2,5	-1	10347	good	8	0	20	80	left	-5	-13	all	16	270	150-210	50
130906	tao-cueRF-hay-514-001+01	1a	1	-2,7	-1,2	10227	good	8	0	20	80	left	-5	-13	16	16	240	240-300	50
130906	tao-cueRF-hay-514-001+01	1b	1	-2,7	-1,2	10227	good	8	0	20	80	left	-5	-13	4	16	240	270	50

Additional supplementary materials 3: Example epars & mpars

Note: The epars define the time sequence of the experiment, the location of the stimulus, i.e. when and where to show the stimulus on the screen. The epars also on-line control the data collection and some events related to subject performance (such as eye position, time window of reaction etc.). The mpars controls the properties of the stimuli, such as the motion direction, speed, dot density, color of the RDP.

Example epars:

Experiment 1
cueRF.epar

```
projectLeader tao
expCode cueRF
displayWindowOnSecondMonitor 0 0 200 200
trialProtocol 1 15
0 0 0 0 1 0
55   0  -40 -360   1   1
10   20  -40 -360   1   1
1 0 0 0 0 0
55   0  -40  360   1   1
10   20  -40  360   1   1
105 0 0 0 1 1
55   59  -40 -360   1   1
55   59  -40  360   1   1
55   0  -40 -360   1   0
55   0  -40  360   1   0
55   59  -40 -360   1   0
55   59  -40  360   1   0
10   20  -40 -360   1   0
10   20  -40  360   1   0
# 2 stimuli in FRF # 3 cue in FRF;
# 4 1st FP; 5 patch opposite to FRF; 6 cue for 5; 7 2nd FP or saccade target;
# 8 and 9 patches removed before saccade in FRF;
# 10 and 11 patches in RF; 12 and 13 patches removed before saccade in RF.
displayCenter 0        1       0.65    0.5
displayCenter 1   1   -600 0
filenames&pathname 37 :traceAtt:traceMpars:
Luminance.mpar
fixStim1.mpar
fixStim2.mpar
Cue.mpar
TP.mpar
T45.mpar
T90.mpar
T135.mpar
T180.mpar
T225.mpar
T270.mpar
T315.mpar
DP.mpar
D45.mpar
D90.mpar
D135.mpar
D180.mpar
D225.mpar
D270.mpar
D315.mpar
AttTP.mpar
AttDP.mpar
DPshort.mpar
fixStimlong.mpar
DPOff.mpar
AttTPF.mpar
AttDPF.mpar
D180Off.mpar
fixStim4.mpar
fixStim5.mpar
fixStim6.mpar
AttTP180.mpar
AttDP180.mpar
AttTPF180.mpar
AttDPF180.mpar
Att4TP.mpar
Att4DP.mpar
# four patches, cue in FRF(class 1-4) or RF(class 6-9)
# class 1 and 2 cue in and cue out contineous, cue in FRF, class 3=1, class 4 = 2
# class 5 and 6 cue in and cue out interrupted, cue in RF
# class 7 and 8 pure saccade
classes 9
1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
1 29 37 0 0 37 0 31 0 0 36 37 0 0 4 0 1 0 0
1 29 37 0 0 37 0 31 0 0 37 36 0 0 0 4 2 0 0
1 29 37 0 0 37 0 31 0 0 36 37 0 0 4 0 3 0 0
1 29 37 0 0 37 0 31 0 0 37 36 0 0 0 4 4 0 0
1 2 0 0 0 0 0 3 25 25 0 0 25 25 4 0 5 0 0
1 2 0 0 0 0 0 3 25 25 0 0 25 25 0 4 6 0 0
1 2 0 0 0 0 0 3 0 0 0 0 0 0 0 0 7 0 0
1 2 0 0 0 0 0 3 0 0 0 0 0 0 0 0 8 0 0
classFrequencyOption 0
# default is zero, this equates the number of trials
waitForLever 10000
rewardDuration 90
```

leverDownRewardDuration 0
preLeverBeepDelay 2000
anticipatedResponseDuration 150
responseTimeWindow 600
#changed above from 500
hitDelay 1500
missDelay 1000
leverReleaseDuration 600
juicePin 1
fixpointIndexColor 255
backgroundIndexColor 200
fixPointSize 12
keyboardResponse FALSE
earlyResponsePermitted FALSE
fixPointVisibleBetweenTrials false
fixationRequired FALSE
collectEyePositions TRUE
fixAreaRadiusOfClass 0 80
preLeverFixRelaxation 2
smoothEyePositions 4
spikeSource 1
sampleSource 1
collectSpikes TRUE
numberOfTrials 9000
dotPosToBuffer FALSE
spikeRecSystem 3
eyePosDecay -20
provideWords TRUE
openDataFile
savePupilDiameter TRUE

Experiment 2

cueFRF.epar

projectLeader tao
expCode cueFRF
displayWindowOnSecondMonitor 0 0 200 200
trialProtocol 1 15
0 0 0 0 1 0
55 0 -40 -360 1 1
10 20 -40 -360 1 1
1 0 0 0 0 0
55 0 -40 360 1 1
10 20 -40 360 1 1
105 0 0 0 1 1
55 59 -40 -360 1 1
55 59 -40 360 1 1
55 0 -40 -360 1 0
55 0 -40 360 1 0
55 59 -40 -360 1 0
55 59 -40 360 1 0
10 20 -40 -360 1 0
10 20 -40 360 1 0
2 stimuli in FRF # 3 cue in FRF;
4 1st FP; 5 patch opposite to FRF; 6 cue for 5; 7 2nd FP or saccade target;
8 and 9 patches removed before saccade in FRF;
10 and 11 patches in RF; 12 and 13 patches removed before saccade in RF.
displayCenter 0 1 0.34375 0.5
displayCenter 1 1 600 0
filenames&pathname 37 :traceAtt:traceMpars:
Luminance.mpar
fixStim1.mpar
fixStim2.mpar
Cue.mpar
TP.mpar
T45.mpar
T90.mpar
T135.mpar
T180.mpar
T225.mpar
T270.mpar
T315.mpar
DP.mpar
D45.mpar
D90.mpar
D135.mpar
D180.mpar
D225.mpar
D270.mpar
D315.mpar
AttTP.mpar
AttDP.mpar
DPshort.mpar
fixStimlong.mpar
DPOff.mpar
AttTPF.mpar
AttDPF.mpar
D180Off.mpar
fixStim4.mpar
fixStim5.mpar
fixStim6.mpar
AttTP180.mpar
AttDP180.mpar
AttTPF180.mpar
AttDPF180.mpar
Att4TP.mpar
Att4DP.mpar
class 1 and 2 & class 3 and 4 cue in and cue out contineous, cue in FRF
class 5 and 6 cue in and cue outinterrupted, cue in RF
class 7 and 8 pure saccade
class 9 and 10 stimuli in FRF, no stimuli in RF, sever as control for response to stimuli in FRF
classes 11

1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
1 29 36 4 0 37 0 31 0 0 37 37 0 0 0 0 1 0 0
1 29 37 0 0 36 4 31 0 0 37 37 0 0 0 0 2 0 0
1 29 36 4 0 37 0 31 0 0 37 37 0 0 0 0 3 0 0
1 29 37 0 0 36 4 31 0 0 37 37 0 0 0 0 4 0 0
1 2 0 4 0 0 0 3 25 25 0 0 25 25 0 0 5 0 0
1 2 0 0 0 0 4 3 25 25 0 0 25 25 0 0 6 0 0
1 2 0 0 0 0 0 3 0 0 0 0 0 0 0 0 7 0 0
1 2 0 0 0 0 0 3 0 0 0 0 0 0 0 0 8 0 0
1 30 36 4 0 37 0 0 0 0 0 0 0 0 0 0 9 0 0
1 30 37 0 0 36 4 0 0 0 0 0 0 0 0 0 10 0 0

classFrequencyOption 0
default is zero, this equates the number of trials
waitForLever 10000
rewardDuration 90
leverDownRewardDuration 0
preLeverBeepDelay 2000
anticipatedResponseDuration 150
responseTimeWindow 600
#changed above from 500
hitDelay 1500
missDelay 1000
leverReleaseDuration 600
juicePin 1
fixpointIndexColor 255
backgroundIndexColor 200
fixPointSize 12
keyboardResponse FALSE
earlyResponsePermitted FALSE
fixPointVisibleBetweenTrials false
fixationRequired FALSE
collectEyePositions TRUE
fixAreaRadiusOfClass 0 80
preLeverFixRelaxation 2
smoothEyePositions 4
spikeSource 1
sampleSource 1
collectSpikes TRUE
numberOfTrials 9000
dotPosToBuffer FALSE
spikeRecSystem 3
eyePosDecay -20
provideWords TRUE
openDataFile
savePupilDiameter TRUE

Example mpars:

fixStim1.mpar
numberOfSurfaces 1 40 0
pixelradius 20
numberOfFrames 105
#qtRGBForeColor 6553 6553 0
qtIndexForeColor 255
qtSquare -6 -6 6 6

fixStim2.mpar
numberOfSurfaces 1 40 0
pixelradius 10
numberOfFrames 105
#qtRGBForeColor 6553 6553 0
qtIndexForeColor 255
qtSquare -6 -6 6 6
qtSuspendFix 105 125
qtFixFactor 105 -1 1.5
qtFixDispCtr 105 -1 1

fixStim4.mpar
numberOfSurfaces 1 40 0
pixelradius 10
numberOfFrames 105
#qtRGBForeColor 6553 6553 0
qtIndexForeColor 255
qtSquare -6 -6 6 6
qtSuspendFix 105 125
qtFixFactor 105 -1 1.5
qtFixDispCtr 105 -1 1

fixStim6.mpar
numberOfSurfaces 1 40 0
pixelradius 10
numberOfFrames 300
#qtRGBForeColor 6553 6553 0
qtIndexForeColor 255
qtSquare -6 -6 6 6
qtSuspendFix 105 125
qtFixFactor 105 -1 1.5
qtFixDispCtr 105 -1 1

AttTPF.mpar
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 80
numberOfFrames 250
speed 16
shape circle
colorIndex 255
direction 210
changePhase -60 140
directionTable 2 120 300
changePhase 10 10
direction 210

Att4TP.mpar
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 80
numberOfFrames 250

speed 16
shape circle
colorIndex 255
direction 90
changePhase -20 150
directionTable 2 0 180
changePhase 10 10
direction 90

Att4DP.mpar
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 80
numberOfFrames 250
speed 16
shape circle
colorIndex 255
direction 90
changePhase 20 150
directionTable 2 0 180
changePhase 10 10
direction 90

Chapter 3

Visual attention is available at a task-relevant location rapidly after a saccade

(elife, in press)

Visual attention is available at a task-relevant location rapidly after a saccade

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Abstract

Maintaining attention at a task-relevant spatial location while making eye-movements necessitates a rapid, saccade-synchronized shift of attentional modulation from the neuronal population representing the task-relevant location before the saccade to the one representing it after the saccade. Currently, the precise time at which spatial attention becomes fully allocated to the task-relevant location after the saccade remains unclear. Using a fine-grained temporal analysis of human peri-saccadic detection performance in an attention task, we show that spatial attention is fully available at the task-relevant location within 30 milliseconds after the saccade. Subjects tracked the attentional target veridically throughout our task: i.e. they almost never responded to non-target stimuli. Spatial attention and saccadic processing therefore co-ordinate well to ensure that relevant locations are attentionally enhanced soon after the beginning of each eye fixation.

Introduction

The processing of vision and visuospatial attention mostly proceeds via retinotopic representations in the brain [1, 2]. Since each saccadic eye-movement leads to a change in the retinotopic representation of the visual scene, maintaining attention at a task-relevant spatial location across a saccade necessitates a rapid, saccade-synchronized shift of attentional modulation from the neuronal population representing the task-relevant location before the saccade to the one representing it after the saccade [3, 4]. Currently, perceptual measurements in humans suggest a neuronal attention shift that starts before the saccade and continues after the saccade ends [5-10]. However, because these previous measurements used coarse temporal sampling and/or long-duration attentional probes, the precise time at which spatial attention becomes fully allocated to the task-relevant location after the saccade remains unclear. Here, using a fine-grained temporal analysis of human peri-saccadic detection performance in an attention task, we show that spatial attention is fully available at the task-relevant location within 30 milliseconds after the saccade. This rapid post-saccadic recovery of performance in our attention task indicates that retinotopic attentional shifts occur within the time required to recover from saccadic suppression of vision. Subjects almost never responded to the distractor change, indicating that they tracked the attentional target veridically throughout the task. Spatial attention and saccadic processing therefore co-ordinate well to ensure that relevant locations are attentionally enhanced soon after the beginning of each eye fixation.

Results and Discussion

We measured human peri-saccadic attentional allocation by combining an endogenous spatial attention task with a visually-guided saccade. Human subjects had to make a saccade to follow a fixation point when it jumped to a new location, and concurrently, pay attention throughout the trial to a target moving random-dot pattern (RDP) presented eccentrically among three or five physically similar distractor RDPs (Figure 1, and Experimental Procedures). We measured the subjects' attentional allocation by their ability to detect a brief (23.5 ms) change in target motion, while ignoring similar changes in the distractors. The target and distractor changes occurred at different times around the saccade, allowing us to report for the first time, peri-saccadic performance in an attention task with fine-grained temporal precision. The intervening saccade poses a challenge for the attentional system, because due to the retinotopic shift of the target location across the saccade, the attentional system needs to shift its modulatory influence from the neuronal population representing the target before the saccade to the neuronal population representing the target after the saccade. By using a fixed timing and location for the fixation point jump, we could isolate the dynamics of this attentional remapping process and minimize its interaction with the dynamics of attentional allocation to other exogenous visual events. We therefore made the saccade spatially and temporally predictable by having the fixation point jump at the same time and to the same location on each trial so that the subject could best focus on the target pattern.

In Experiment 1, we looked at the peri-saccadic performance of 8 subjects (pooled data in Figure 2A, individual subject-data in Figure 2 - figure supplement 1). At times well before and well after the saccade, subjects almost always detected the target change and their performance was near 100%. Performance began to drop around the time the fixation point jumped (dashed vertical line in Figure 2A), as expected from the previously reported diversion of pre-saccadic attentional resources towards the saccade task [11-13] and the post-saccadic retinotopic location [6]. The performance then dropped steeply right before the saccade, as expected from the drop in visual sensitivity due to saccadic suppression [14-16]. Importantly, our data show (for the first time in an attention task, to our knowledge) that performance recovered back to baseline within 30 ms of saccade offset (Figure 2A). The rapid post-saccadic recovery of performance indicates that attention is allocated to the task-relevant location within 30 ms after the saccade ends. The rapid time-course of recovery resembles that previously shown for saccadic suppression of visual performance in tasks where visual sensitivity was probed around a saccade using a briefly flashed change, but without any requirement to maintain attention on a target across a saccade [14-16]. This suggests that while resumption of visual function after a saccade is constrained by the recovery from saccadic suppression [17], the peri-saccadic attentional shift necessitated by retinotopic visual processing does not impose an additional temporal cost on this recovery. The rapid post-saccadic attentional availability at the target location that we infer from our data is consistent with the only physiological data on this issue: in a mental curve-tracing task similar to ours with a fixed attentional target, attentional effects in monkey V1 emerge approximately 80 ms after the end of the

saccade [18]. Given an onset latency of approximately 30 to 50 ms in monkey V1, MT and LIP [18-20], a change occurring 30 ms after saccade offset would reach the visual cortex at approximately the time when its neurons representing the target after the saccade are attentionally enhanced.

It is possible that though we report a rapid recovery in Experiment 1, the true recovery was actually slower, but was masked by the fact that performance had already reached its maximum value of 100% within 30 ms of saccade offset. We therefore performed a similar experiment (Experiment 2) with two task difficulties, where peak performance on the harder task was clearly below 100% (Figure 2B). Once again, performance recovered to baseline levels within 30 ms of saccade offset in both the easier and the harder task, indicating that our estimate of a rapid recovery time for performance was genuine and not an artifact due to a ceiling effect. The recovery time-course after the saccade also did not seem to depend on saccade latency (Figure 3). Very similar performance was observed when we grouped trials based on saccade latency into three groups: putative predictive saccades (latencies from 0 to 75 ms), express saccades (latencies from 75 to 125 ms) and regular-latency saccades (latencies from 125 to 250 ms). This indicates that though various differences between these different kinds of saccades have been noted and these different kinds of saccades have been speculated to arise via different neural pathways [21-27], peri-saccadic attentional shifts seem to proceed with a similar time-course in each case.

If the peri-saccadic attentional shift is not temporally well-synchronized with the saccade, attention will be peri-saccadically allocated to irrelevant spatial

locations. In fact, prior findings measuring discrimination performance for attentional probes at different locations suggest that by about 75 ms before the saccade, attentional enhancement could be seen at the “post-saccadic” retinotopic location (which would be the wrong pre-saccadic spatial location) [5]. Other studies report that after the saccade, attention stays at the pre-saccadic retinotopic location (which would be the wrong post-saccadic spatial location) for up to 100 ms after the saccade [7, 28]. The predictive emergence of attention is consistent with single-neuron data from monkeys showing predictive responses in different attentional control areas of the brain [2, 29], while imaging data from humans have been presented as evidence for persistent retinotopic neural activity [9]. Results from a more recent detailed study indicate that peri-saccadic attentional spread and dynamics may show complex patterns: patterns consistent with predictive shifts, transient retinotopic persistence as well as rapid post-saccadic availability of attention at the task-relevant location were seen [10]. In our data, we found no effect of predictive or delayed shifts on the rate of responding to distractor changes (false-positives). In both Experiments 1 and 2, overall, subjects responded to a distractor change on only 2.2 and 2 % of trials respectively. Distractor changes occurred either at the distractor vertically below the target (a control) or at the distractor to the right of the target (that tested post-saccadic retinotopic persistence of the pre-saccadic attentional focus). In the time interval immediately after the saccade (0-150 ms), the data from both experiments showed no statistically significant increase in the rate of false-positives due to retinotopic persistence (compared to the control location; all p-values >0.16, Boschloo’s test; Supplementary file 1A). An additional experiment (Experiment 3; Figure 2 –

figure supplement 3 and Supplementary file 1B) where we changed the task design to test both pre-saccadic predictive shifts and post-saccadic retinotopic persistence (while making distractor changes more numerous and salient) also led to a false-positive rate of less than 1.4 % and no evidence for an effect of either predictive shifts or retinotopic persistence on the false-positive rate. Subjects thus tracked the attentional target veridically throughout our task, and the peri-saccadic spread of attention to irrelevant spatial locations reported in previous studies does not seem to have any manifest effects in our task. One important difference between our task and previous tasks was that we included only one attended location within each trial, and stimuli at all other locations were distractors that the subject had to ignore. In contrast, the previous tasks required subjects to report a probe stimulus that could appear at any of the stimulus locations. There were no distractor stimuli, and attention was instead manipulated by using a dual-task [5, 7, 28] or using an exogenous cue [10]. The fact that all stimulus locations on each trial were potential targets in the previous studies may have led the subjects to adopt a different attentional-set compared to the subjects in our study. Alternatively, the previous results may have reflected only an attentional effect on probe visibility, while the results in our task may additionally reflect the effect of attention on distractor filtering. In current theoretical accounts of attention [30, 31], the effects of attention on distractor filtering and probe visibility correspond to the distinct effects of attention on selection/weighting and sensory signal enhancement respectively. In this scenario, distractor filtering due to the attentional selection/weighting of sensory signals across the visual field is well-synchronized to the saccade and therefore does not spread to irrelevant spatial locations. In contrast,

attentional signal enhancement, but not distractor filtering, is influenced by the predictive shifts and post-saccadic retinotopic persistence of attentional modulation in the brain. As a result, in the previous tasks without a distractor filtering component, the perceptual visibility of probes at irrelevant locations was improved. In our task, any enhanced sensory signal from distractor locations would continue to be down-weighted and filtered out and the subjects would not respond to them. We emphasize that this is only one plausible explanation, and theoretical models of attention are sufficiently complex and flexible to admit alternative explanations. Even more generally, the observed differences could be a result of task-dependent (or even entirely different) attentional mechanisms operating in the different tasks. Extensive measurements and model-testing will be necessary to disambiguate the different possibilities.

Our data represent an important advance in the ongoing discussion about the shifts of spatial attention around the time of a saccade [1, 3, 32-34]. We provide the first temporally fine-grained measurements of detection performance in an attention task in the critical immediate post-saccadic period (0 to 100 ms following saccade offset). Our data show that performance fully recovers soon after the end of the saccade, indicating that the correct stimulus is attended to during this immediate post-sacadic period when visual sensitivity is known to be highest [35]. The rapid time-course of recovery resembles the time-course previously shown for the recovery of visual function from saccadic suppression, suggesting that the retinotopic attentional shift does not impose an additional temporal cost on the resumption of visual function after a saccade. Further, our data indicate that

under our task conditions, subjects very rarely confuse a distractor stimulus for the target. Spatial attention and saccadic execution thus appear to co-ordinate well to ensure that relevant objects are attentionally enhanced soon after the beginning of each eye fixation. These findings are likely to lead to a much better understanding of the impact of peri-saccadic changes in neural activity on visual processing.

Materials and Methods

We measured peri-saccadic attentional allocation by combining a spatial attention task with a visually-guided saccade. We asked human observers to make a saccade to a visual target, and within the same trial, also report a speed and direction change in a target moving random-dot pattern (RDP), while ignoring a similar change in one of the simultaneously-presented distractor RDPs. The target and distractor changes occurred at different times around the saccade, allowing us to measure peri-saccadic attentional performance with fine-grained temporal precision.

Human Subjects

10 subjects (4 males, 6 females, ages 21-30 years) participated in the study, including two of the authors (MK and TY). 8 of the subjects (excluding the two authors) were naïve to the purpose of the experiment. 8, 5 and 4 subjects participated in Experiments 1, 2 and 3 respectively; of these, 3 subjects (including the author MK) participated in all 3 experiments. All subjects were right-handed and reported normal or corrected to normal vision. All naive participants received monetary compensation for each session. Each subject started the experiment with a training session to become familiar with the tasks. The experiments were performed in several blocks over one or two days. Subjects were given verbal and written instructions about the task. The study was performed in accordance with institutional guidelines for experiments with humans, adhered to the principles of the Declaration of Helsinki and was approved by the Ethics

Committee of the Georg-Elias-Müller-Institute of Psychology, University of Göttingen. Each subject gave informed written consent prior to participating in the study.

Apparatus

Subjects were seated in a dimly lit room at a viewing distance of 57cm from the screen with their head resting on a chin and forehead-rest. The only light source in the room was the light from the display monitor. A computer keyboard was used for recording subject responses. All aspects of the experiment were controlled by custom software running on an Apple Macintosh computer. The eye-position was monitored by an infra-red video-based eye-tracker (iView X software running on a SMI Hi-Speed 1250 tracker, SMI GmbH, Germany) at 1000 Hz. The stimuli were displayed on a 1600 by 1200 pixels (40 by 30 degrees) CRT monitor with a fresh rate of 85 Hz. The display background was always grey (40 cd/m^2), and all the visual stimuli were black (0.7 cd/m^2).

Task design

We describe Experiment 1 first: Experiments 2 (Figure 2B) and 3 (Figure 2 - figure supplement 3) are variants of Experiment 1.

Experiment 1: Each trial was started by the subject pressing the space-bar. A fixation point appeared on the screen and subjects maintained their gaze within 2 degrees of this point. The subjects concurrently performed a spatial

attention task and a saccade task on each trial: they were instructed to pay attention to the target RDP and make a saccade if the fixation point jumped to a new location. For the spatial attention task, after 647 ms of fixation, four circular moving random-dot patterns (RDPs: each presented within a circular aperture of 2 degree radius, with dots moving upwards with a speed of 8 degrees of visual angle per second; dot density=10 dots per deg^2), were displayed on the screen. Individual RDP dot size was 0.15 degrees x 0.15 degrees. The subjects were instructed that the RDP at a pre-specified location (3.5 degrees to the right and 4 degrees above the fixation point: Figure 1) was the target: they had to pay attention to that stimulus throughout the trial in order to respond by pressing the downward-arrow key within 600 ms when they detected a brief 2-frame (23.5 ms) speed and direction-change in the target RDP. For these two frames, the RDP dots moved faster at 16 degree per second and horizontally either to the left or the right, and then resumed motion with the original speed and direction. Any changes in the distractor RDPs were to be ignored. The median reaction-time was 324 ms. The second RDP was placed 7 degrees to the right of the target RDP so that post-saccadically, it had the same retinotopic location as the target RDP did pre-saccadically. The other two RDPs were placed at corresponding locations in the lower hemifield. A target RDP change occurred on about 90 % of the trials and between 118 to 1882 ms after RDP onset; the remaining trials were catch trials and no change occurred. A distractor change occurred before the target change on about 39 % of trials, over a similar range of times but at least 400 ms before the target change: the subject had to ignore these changes. Only one target change and possibly also one distractor change occurred on each trial. The distractor change could occur either at

the RDP to the right of the target (with a post-saccadic retinotopic location identical to the target's pre-saccadic retinotopic location) or the RDP below the target. For the saccade task, the fixation point jumped to a new location 7 degrees horizontally to the right of the fixation point 1235 ms after the fixation point appeared. The subjects had to make a single saccade within 553 ms of the fixation point jump to fixate the saccade target location and then maintain their gaze within 2 degrees of the saccade target for the remainder of the trial. Most saccades occurred with a much shorter latency (Figure 3). The use of a predictable time at which the fixation point jumped was advantageous because subjects could focus their attention better on the target RDP without worrying about the temporal uncertainty about when the fixation point would jump. Trials were terminated when the subject pressed the downward arrow key, broke fixation or failed to press a key within 600 ms of a change in the target RDP. Subjects received no other feedback about trial outcome. The use of a 2 degree fixation window during the two fixation periods was not critical. We also obtained similar results when using a narrower fixation window of 0.5 degrees: we ensured that the eye did not deviate by more than 0.5 degrees from the median horizontal and vertical eye-position during fixation on each trial (Figure 2 – figure supplement 5). Using the median eye-position compensates for across-trial drifts in calibration and is based on the standard calibration assumption that normal-viewing subjects will foveate a visual target when asked to fixate on it and therefore, their eye-position variability will be centered on the fixated location.

Experiment 2: This was similar to Experiment 1, with the following key differences. Two task difficulties were used and the change involved only a

motion direction change, without a speed change. The two task difficulties were created by using two magnitudes of direction change for each subject; these magnitudes were chosen in a separate calibration session,where the overall detection performance was estimated for nine direction-change magnitudes between 20 and 90 degrees. The calibration session used a fixation task similar to the task in Experiment 2 except that no saccade was required. The direction-changes that led to approximately 70 % and 90 % detection performance were chosen for Experiment 2. Across subjects, the direction-change varied between 35 and 60 degrees for the hard task and between 50 and 90 degrees for the easier task. Also, to make more of the target changes occur peri-saccadically, the timing of the task was slightly modified so that the RDPs came on at 412 ms after fixation point onset (Figure 1), and the target motion change occurred from 235 ms to 1647 ms after RDP onset; approximately 27 % of trials had a distractor change before the target-change over a similar time-frame (118 ms to 1224 ms, with the same constraint of a 400 ms separation from the target-change as in Experiment 1). About 7 % of trials were catch trials.

Experiment 3: This was also similar to Experiment 1, except that we used 2 additional distractor RDPs, giving a total of 6 RDPs instead of 4. One of the additional RDPs was placed seven degrees to the left of the target RDP, which is the location to which attention would be expected to predictively switch just before the saccade. The other RDP was placed eight degrees below this RDP, in line with the other RDPs in the lower hemifield. Further, to make the distractor changes more salient and improve the chances of a false-positive, the speed now increased during the motion change from 4 to

32 degrees per second (instead of 8 to 16 degrees per second in Experiment 1); the direction-change remained at 90 degrees (vertically upward to horizontal towards the left or the right). The range of target change times was slightly delayed compared to Experiments 1 and 2 so that a distractor change could occur more often before a target change and a false positive potentially elicited: the target changes in Experiment 3 could occur from 412 to 2176 ms after RDP onset. The distractor change occurred from 470 to 941 ms after RDP onset so that the distractor changes now occurred more often (about 60 % of target-changes were now preceded by distractor changes) and mostly before the saccade. Distractor changes occurred either to the right of the target (to measure post-saccadic retinotopic persistence) or to the left of the target (to measure pre-saccadic predictive shifts). About 6 % of trials were catch trials.

Data analysis

Data processing was done using MATLAB (Mathworks Inc, Natwick, MA), except for the exact test of binomial proportions performed using the Exact package [36] in R [37]. We detected saccades using a standard velocity-threshold algorithm: onset (and offset) times were determined by when the eye velocity exceeded (and then dropped below) an individualized threshold (set to between 40 and 70 degrees per second, fixed for each subject). This threshold value was set to lie clearly above the peak excursions of the baseline noise in the eye-velocity traces, and the algorithm was validated by visual inspection for each subject. By considering the saccade to have ended when the velocity dropped below a threshold value well above the baseline

noise (and when the eye was still moving), our threshold criterion provides a conservative, i.e. early definition of saccadic end-point and therefore a longer estimate of the recovery time for perceptual performance. Our threshold-setting detected the primary saccade close to its end, but excluded post-saccadic dynamic overshoots or glissades [38, 39]. Setting a lower threshold and including these small eye-movements led to an even lower estimate of the recovery time of spatial attention (around 20 ms, instead of the 30 ms we report). We only included trials where the subjects made a single saccade to the saccade target, and this saccade was made between 50 ms before and 450 ms after the time when the fixation point jumped. While these limits are arbitrary, they are not critical and our results remain robust for other reasonable choices, consistent with the lack of an effect of saccade latency on performance (Figure 3).

Trials with a fixation break were excluded from further analysis. Early responses before the target-change were extremely rare: early responses constituted only 1.2, 1 and 0.7 % of trials in Experiments 1, 2 and 3 respectively, even when counting all early responses that were potentially responses to the distractor change in this number. Responses to the distractor change (false-alarms; see Results and Discussion) were also extremely rare; we considered all early responses within 800 ms of a distractor change as a response to the distractor. We could therefore exclude trials with early responses as well and simply define performance using the hit-rate (the proportion of target-changes that were correctly detected). We plotted the performance as a function of the time of target-change relative to saccade offset: since the speed and direction-change lasted 2 frames (at a

refresh rate of 85 Hz), we used the timing of the second frame to define the time of target-change since this was the conservative choice given our focus on the rapid performance recovery after the saccade. For the pooled analyses (Figures 2, 3 and Figure 2 – figure supplement 3A), we pooled the trials from all subjects and then calculated the mean and 95 % Wilson-score confidence intervals [40] over successive non-overlapping time-bins of the X-axis variable (10 ms in Figure 2A, 20 ms in Figure 2B, 50 ms in Figure 3 and 10 ms in Figure 2 - figure supplement 3A). To estimate the time at which performance recovered to its post-saccadic baseline, we first estimated the baseline performance (proportion of correct trials) from 100 to 500 ms following saccade offset and then compared this value (using Boschloo's exact test of binomial proportions and a one-sided p-value for the peri-saccadic performance being lower than the baseline performance) to the performance in successive non-overlapping 10 ms time-bins from 0 to 100 ms following saccade offset. The starting-point of the first non-significant bin (i.e. $p>0.1$) was taken as the time of recovery. Using a one-sided p-value and a cutoff of 0.1 are both conservative choices in our situation since they would only increase the estimated time of recovery. Using a cutoff of $p>0.05$ for non-significance reduced the estimated time of recovery in Experiment 1 (Figure 2A) to 20 ms, but did not affect any of the other estimates. Similarly, the use of Boschloo's test also increases the power to detect a significant difference, and is therefore conservative for our purposes [41, 42]. The time estimated using 10 ms bins was further confirmed with a similar procedure using 5 ms bins. In all cases (Figures 2A,2B and 3), the estimated value was 30 ms, meaning that the performance in the time-bin from both 30 to 35 ms and 30 to 40 ms was not significantly different from baseline. For Experiment

1 (Figure 2A), there were at least 48 trials in each 10 ms time-bin from 0 to 40 ms. For the other experiments, the values were: Experiment 2 (Figure 2B) - 42 trials for the easy task, and 39 trials for the hard task and Experiment 3 (Figure 2 – figure supplement 3) - 31 trials. These trial numbers gave us 80 % power to detect a reduction to 90 % (Experiment 1), 90 % (Experiment 2, easy), 81 % (Experiment 2, hard) and 83 % (Experiment 3) of the baseline value, and the estimated recovery times agreed well with the values one would estimate based on visual inspection of the curves. For the individual subjects (Figure 2 - figure supplements 1-3), the time-courses appear very similar to the pooled averages. However, formal statistical testing was precluded by the small number of trials in each bin, since the estimates of recovery time based on statistical significance would be shorter than the estimate for the pooled averages (and therefore anti-conservative). We therefore marked the estimated time at which the performance reached 80 % of the baseline probability on the individual subject plots in Figure 2 – figure supplements 1 to 3. This value was calculated via simple linear interpolation and by visual inspection, captures the time-course of recovery quite well. We collected data from a planned number of 8 subjects in Experiment 1. Since the data from the 8 subjects in Experiment 1 showed very similar time-courses, we collected data from a smaller number of 5 and 4 subjects respectively in the additional experiments (2 and 3).

Author contributions

TY and BSK designed the study; TY and MK conducted the experiments; TY, MK and BSK analyzed the data; ST commented on the manuscript; TY and BSK wrote the manuscript.

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Legends

Figure 1. Task-design and timing. Human subjects performed a task that involved attending to a target (marked with a white T and always at the same location) presented as one among four (A) or six (B) moving RDPs while also making a visually guided saccade if the fixation point jumped seven degrees to the right (1235 ms after trial onset). The subjects were instructed to respond with a key-press when the target RDP briefly changed speed and direction, but to ignore similar changes in any of the remaining RDPs. Target and distractor changes occurred at different times around the saccade, enabling the measurement of peri-saccadic performance in this attention task. Two different task-difficulties were used in Experiment 2, while six RDPs were used in Experiment 3 instead of four. There were also minor differences in timing between the three tasks.

Figure 2. Rapid post-saccadic recovery of performance. A) Detection-performance (hit-rate) of motion-direction drops around the time of the saccade and recovers within 30 ms after the saccade. The figure shows the mean detection-performance (and 95 % confidence bands) for all trials pooled over 8 subjects calculated in non-overlapping 10 ms time-bins of the abscissa (time of target-change relative to saccade offset). The inset shows the same data, focusing on the time between -100 and 100 ms. Data from individual subjects show little inter-individual variability in the time-course of recovery (figure supplement 1). The triangle indicates the earliest time (30 ms) at which performance is statistically indistinguishable from that over the 100 to 500 ms time-period (using Boschloo's exact test; see Experimental

Procedures). The dashed vertical line indicates the mean time of fixation-point offset and the stippled vertical line indicates the mean saccade onset time. See also figure supplements 1 and 3. B) Similar results were obtained when two different task-difficulties were used (data pooled over 5 subjects). The data from the higher-difficulty task (in red) show that the rapid recovery is not an artifact of a ceiling effect on performance. Data plotted using 20 ms time-bins. Figure conventions as in Figure 2A. See also figure supplement 2 for data from individual subjects. Figure supplements 4 and 5 replot the same data as in Figures 2A and 2B and in the same format, but figure supplement 4 uses the time of target-change relative to saccade onset and figure supplement 5 only includes trials where a fixation window of 0.5 degrees was used (see corresponding legends for details).

Figure 3. Rapid post-saccadic performance recovery is independent of saccade latency. The time-course of recovery was indistinguishable for saccades in three different latency ranges in the same dataset used in Figure 2A (8 subjects, color coding in inset): 0-75 ms (predictive saccades), 75-125 ms (express saccades), 125-250 ms (regular-latency saccades). The inset plots the pooled saccade latency distribution. Figure conventions as in Figure 2A, except that non-overlapping 50 ms time-bins were used.

Figure 2 - figure supplement 1. Individual subjects - rapid post-saccadic recovery of performance. Data from the eight individual subjects whose pooled data appears in Figure 2A. Triangles indicate time at which performance reaches 80 % of baseline (see Supplementary Experimental Procedures); the values of this time are 24, 24, 23, 19, 24, 22, 23 and 35 ms

for Subjects BA, JV, JS, JK, KW, LV, MK and SP respectively. Data plotted using 20 ms time-bins. All other conventions as in Figure 2A. Related to Figure 2A.

Figure 2 - figure supplement 2. Individual subjects - rapid post-saccadic recovery of performance for two task difficulties. Data from the five individual subjects whose pooled data appears in Fig.2B. Triangles indicate time at which performance reaches 80 % of baseline (see Supplementary Experimental Procedures); the values of this time are 25, 24, 29, 30, and 25 ms for the easier task and 29, 40, 32, 30, and 21 ms for the harder task for subjects JV, LV, MK, MS and TY respectively. All other conventions as in Figure 2B. Related to Figure 2B.

Figure 2 – figure supplement 3. Results from experiment 3, where distractor changes are more numerous and more salient also show rapid post-saccadic recovery of performance (within 30 ms), and no evidence for post-saccadic retinotopic persistence or pre-saccadic predictive shifts. Pooled data in A and data from individual subjects in B. Triangles in B indicate time at which performance reaches 80 % of baseline (see Supplementary Experimental Procedures); the values of this time are 28, 35, 30, and 26 ms for subjects JV, JS, LV and MK respectively. All other conventions as in Figure 2A. Related to Figure 2A.

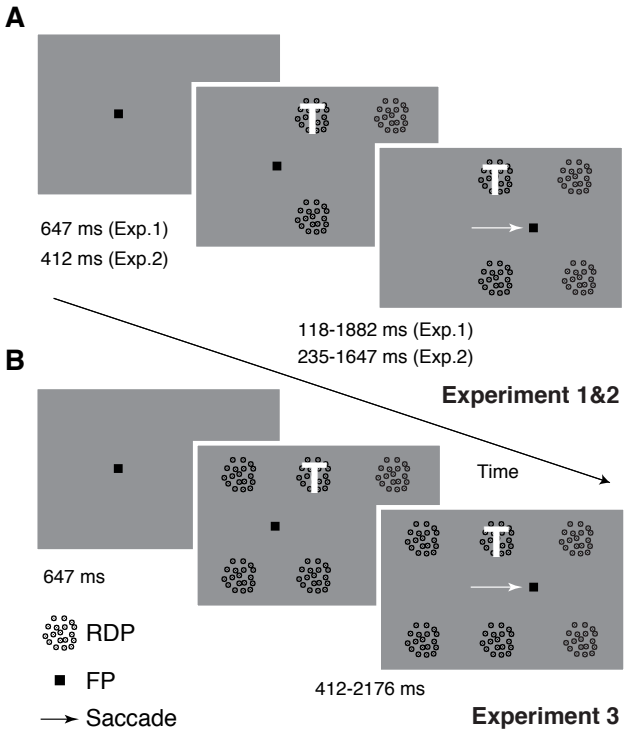
Figure 2 - figure supplement 4. Post-saccadic recovery of performance plotted relative to saccade onset. This figure is identical to Figure 2, except that the performance (in Experiments 1 and 2) is plotted as a function

of the time of target change relative to saccade onset. Recovery times relative to saccade onset are 60 ms in A and 70 ms for both tasks in B. Related to Figures 2A and 2B.

Figure 2 - figure supplement 5. Post-saccadic recovery of performance plotted with a smaller fixation window. This figure is identical to Figure 2, except that we only included trials where the horizontal and vertical eye-positions did not diverge by more than 0.5 degrees during fixation from their median values (see Methods). Estimated recovery times are 20 ms in A and 30 ms for both tasks in B. Despite the much smaller fixation window, A and B include 59 % and 78 % of the trials in Figures 2A and 2B respectively. Related to Figures 2A and 2B.

Supplementary File 1A: Experiments 1 and 2. False-positive rate from 0 to 150 ms after saccade offset shows no effect of post-saccadic retinotopic attentional persistence.

Supplementary File 1B: The false-positive rate in Experiment 3 shows no effect of either pre-saccadic predictive shifts or post-saccadic retinotopic persistence.



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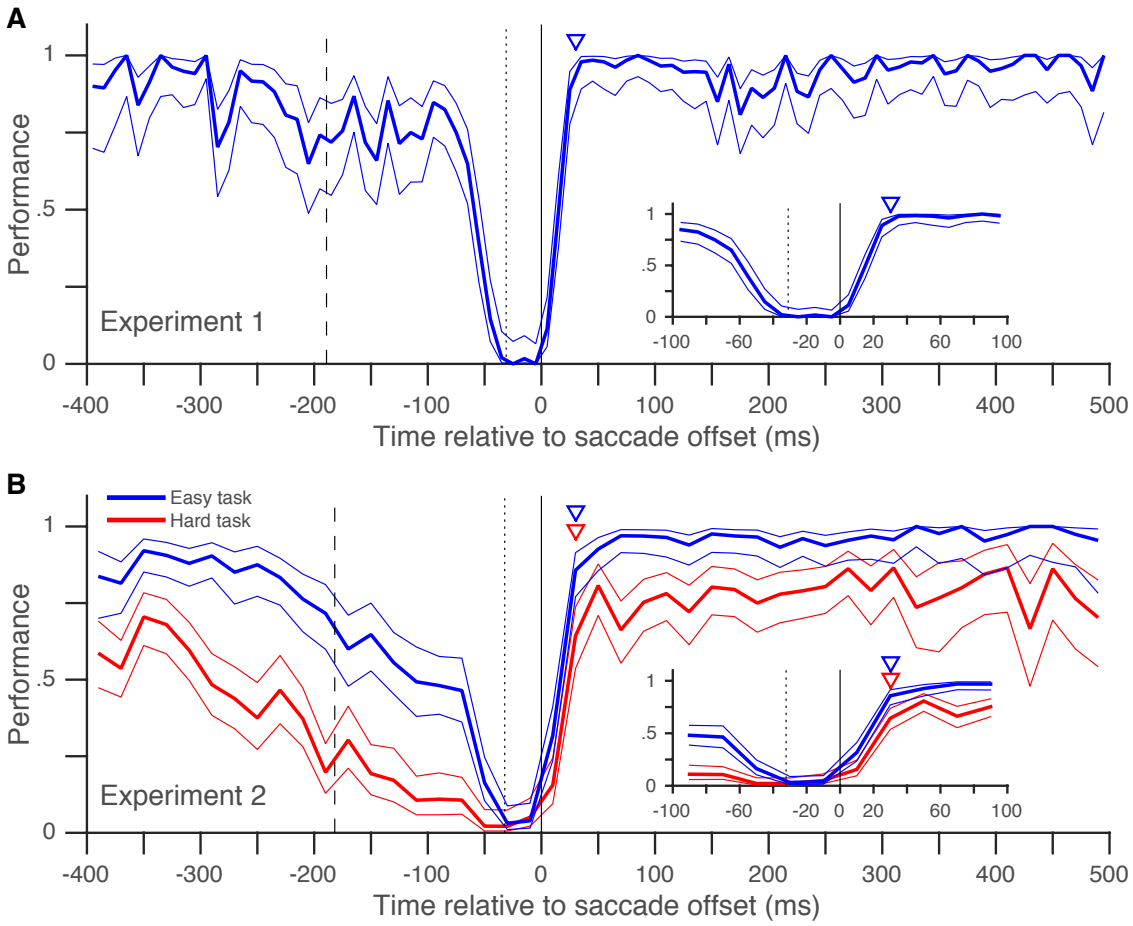

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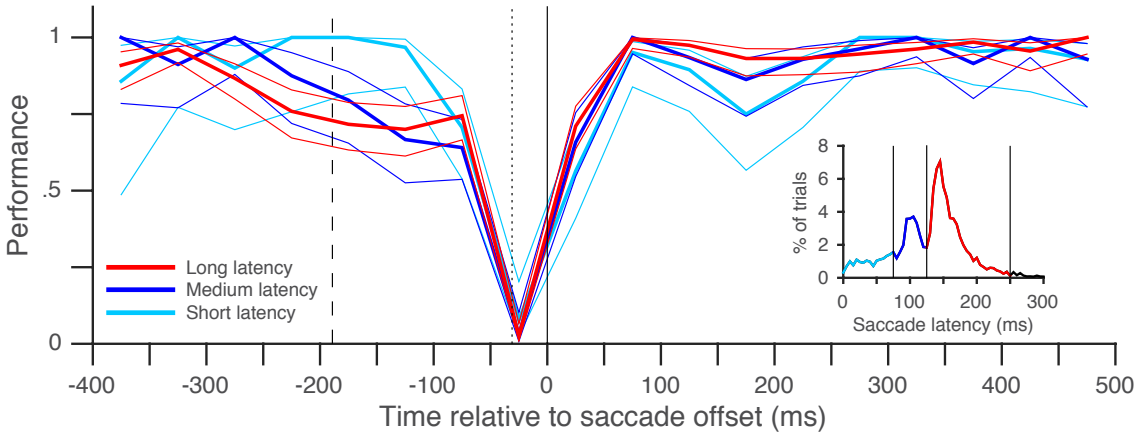

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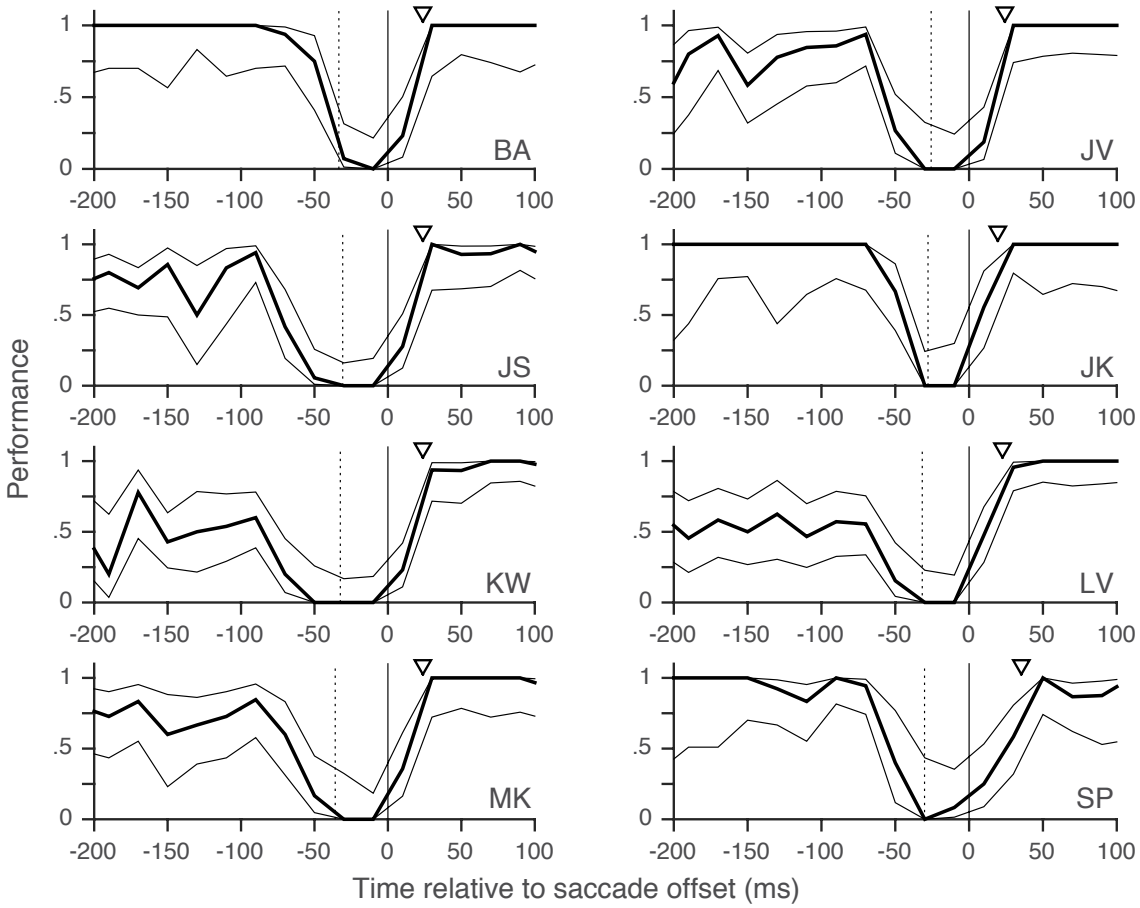


Figure 2 - figure supplement 1. Individual subjects - rapid post-saccadic recovery of performance. Data from the eight individual subjects whose pooled data appears in Figure 2A. Triangles indicate time at which performance reaches 80 % of baseline (see Supplementary Experimental Procedures); the values of this time are 24, 24, 23, 19, 24, 22, 23 and 35 ms for Subjects BA, JV, JS, JK, KW, LV, MK and SP respectively. Data plotted using 20 ms time-bins. All other conventions as in Figure 2A. Related to Figure 2A.

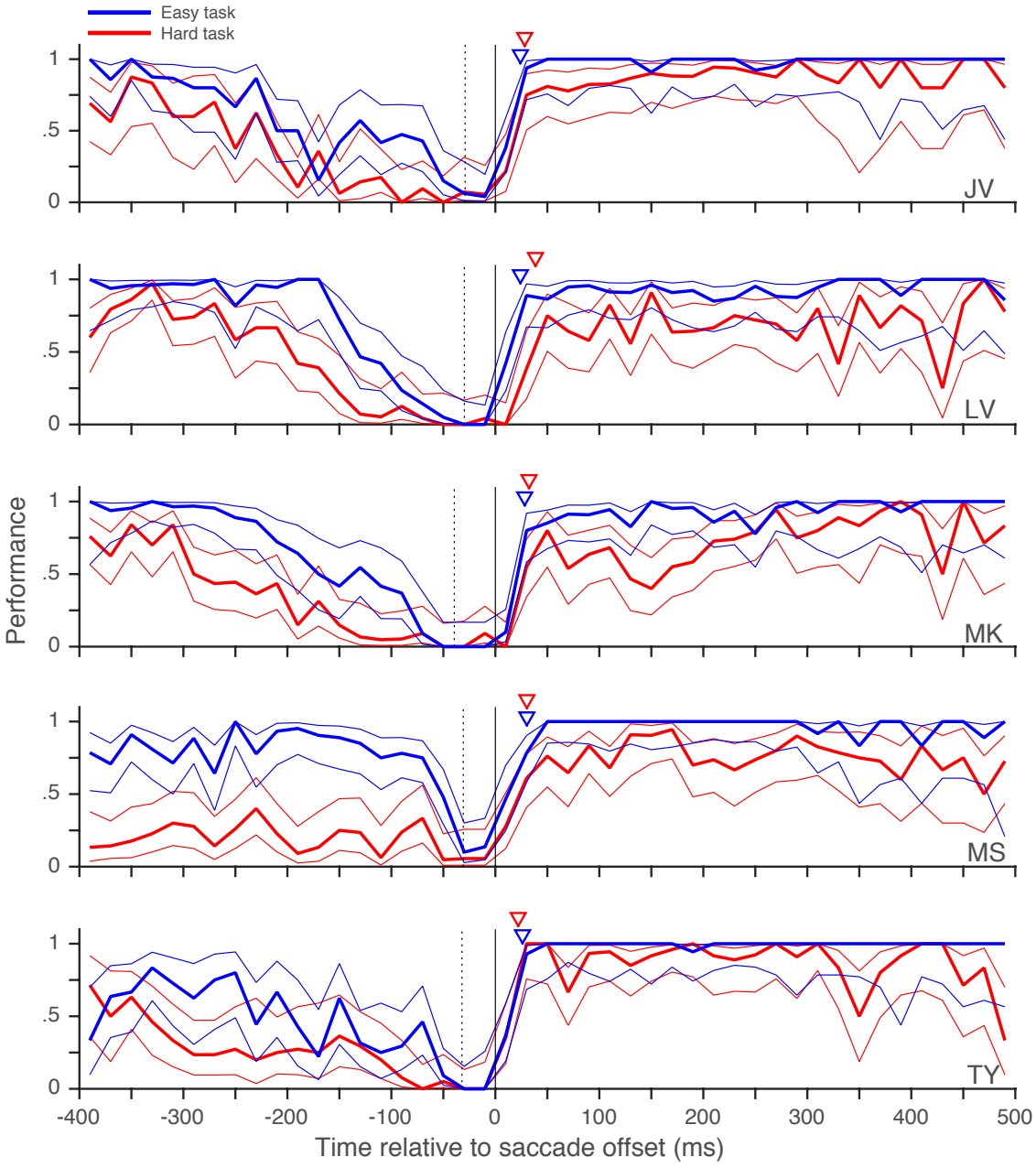


Figure 2 - figure supplement 2. Individual subjects - rapid post-saccadic recovery of performance for two task difficulties. Data from the five individual subjects whose pooled data appears in Fig.2B. Triangles indicate time at which performance reaches 80 % of baseline (see Supplementary Experimental Procedures); the values of this time are 25, 24, 29, 30, and 25 ms for the easier task and 29, 40, 32, 30, and 21 ms for the harder task for subjects JV, LV, MK, MS and TY respectively. All other conventions as in Figure 2B. Related to Figure 2B.

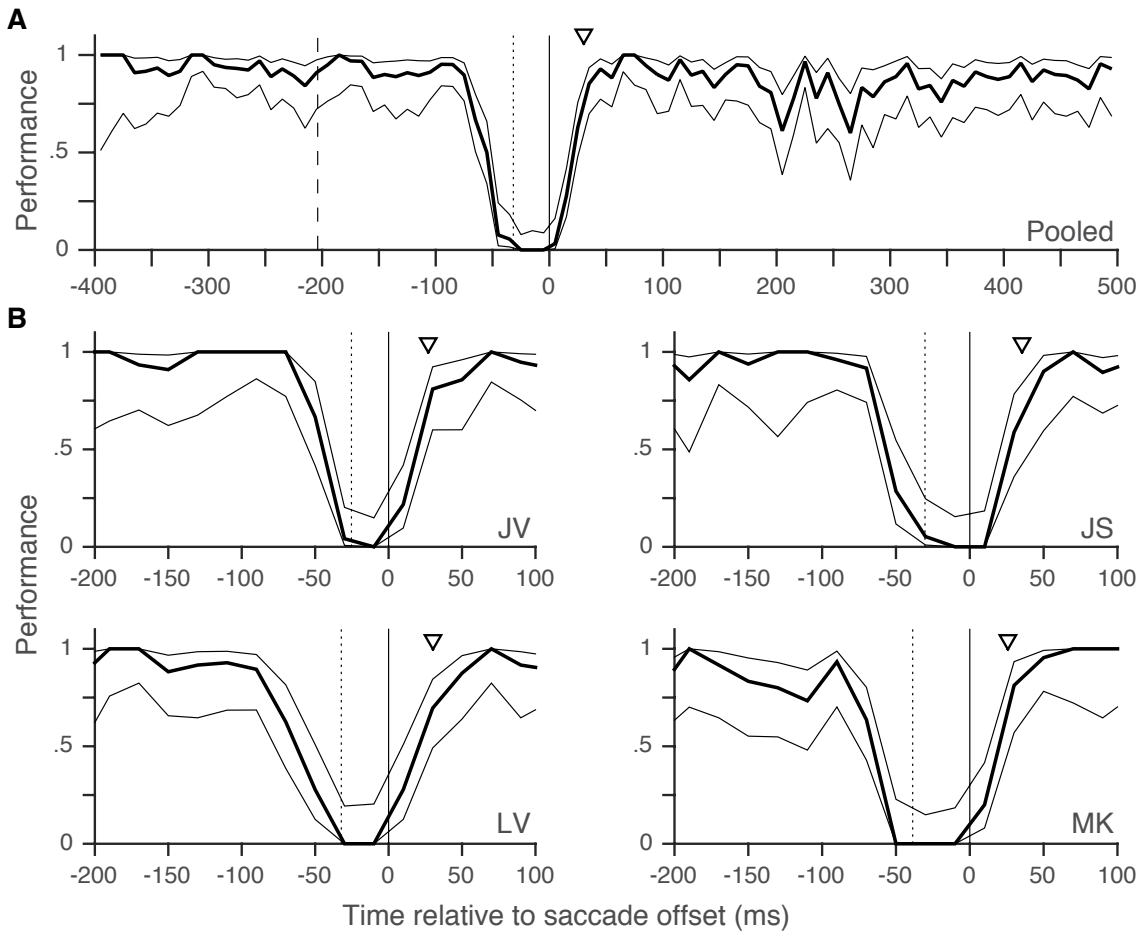
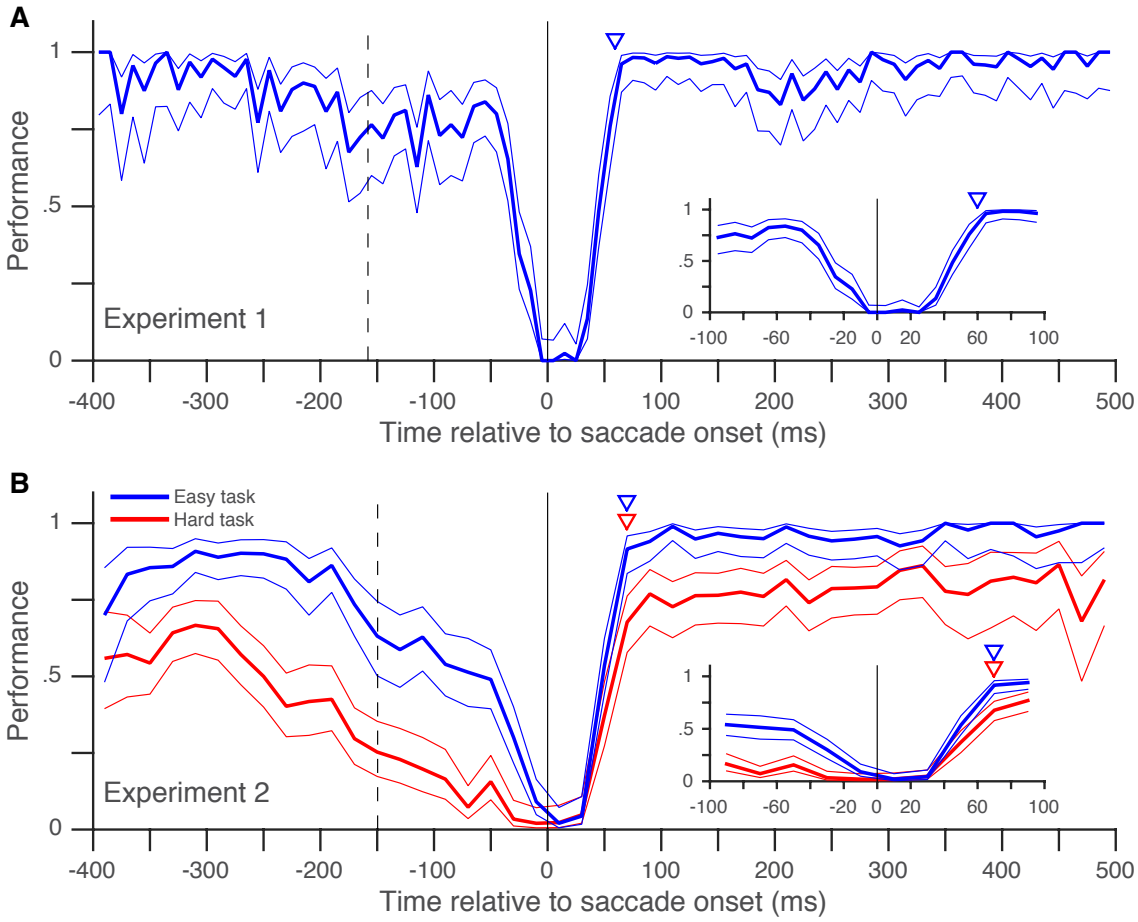


Figure 2 – figure supplement 3. Results from experiment 3, where distractor changes are more numerous and more salient also show rapid post-saccadic recovery of performance (within 30 ms), and no evidence for post-saccadic retinotopic persistence or pre-saccadic predictive shifts. Pooled data in A and data from individual subjects in B. Triangles in B indicate time at which performance reaches 80 % of baseline (see Supplementary Experimental Procedures); the values of this time are 28, 35, 30, and 26 ms for subjects JV, JS, LV and MK respectively. All other conventions as in Figure 2A. Related to Figure 2A.



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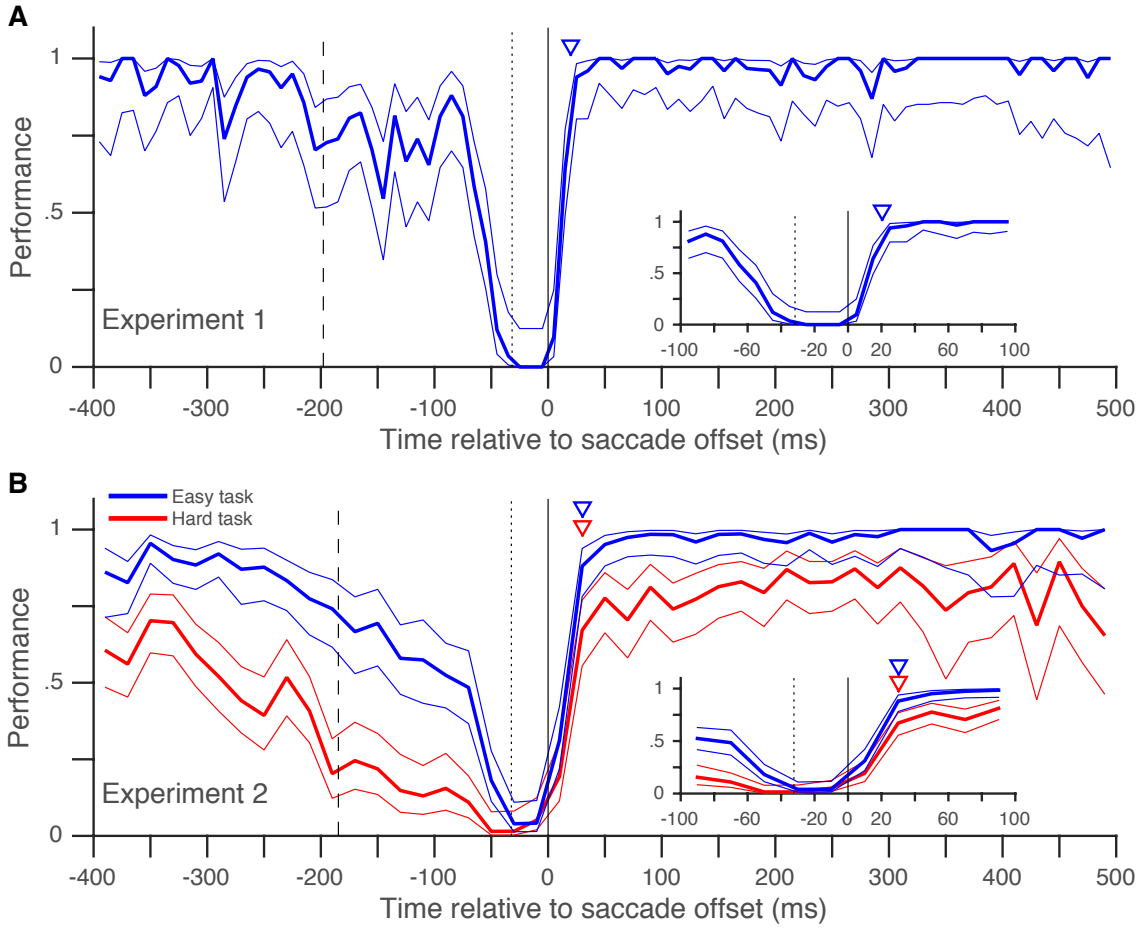


Figure 2 - figure supplement 5. Post-saccadic recovery of performance plotted with a smaller fixation window. This figure is identical to Figure 2, except that we only included trials where the horizontal and vertical eye-positions did not diverge by more than 0.5 degrees during fixation from their median values (see Methods). Estimated recovery times are 20 ms in A and 30 ms for both tasks in B. Despite the much smaller fixation window, A and B include 59 % and 78 % of the trials in Figures 2A and 2B respectively. Related to Figures 2A and 2B.

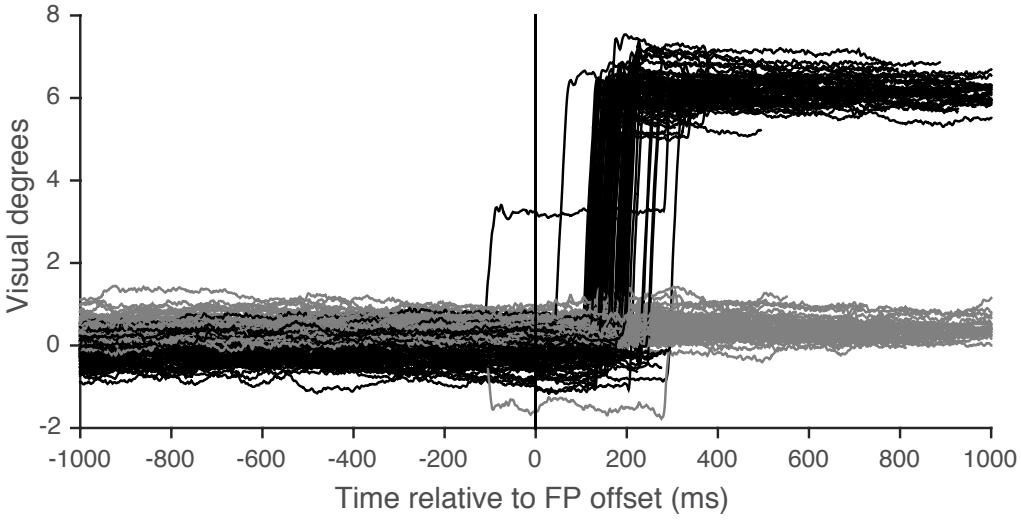
Supplementary File 1A: Experiments 1 and 2. False-positive rate from 0 to 150 ms after saccade offset shows no effect of post-saccadic retinotopic attentional persistence.

	Distractor to right of target (retinotopic persistence)		Distractor below target (control)	
	No. False-positives	Total trials	No. False-positives	Total trials
Experiment 1				
Subject BA	0	16	1	9
Subject JV	0	25	0	12
Subject JS	0	18	0	15
Subject JK	0	17	0	17
Subject KW	1	27	3	21
Subject LV	0	26	0	23
Subject MK	0	10	0	12
Subject SP	4	24	1	18
Total	5	163	5	127
Experiment 2				
Subject JV	1	14	5	14
Subject LV	0	25	0	27
Subject MK	0	15	0	17
Subject MS	6	43	5	61
Subject TY	2	18	0	17
Total	9	115	10	136

Supplementary File 1B: The false-positive rate in Experiment 3 shows no effect of either pre-saccadic predictive shifts or post-saccadic retinotopic persistence.

	Distractor to right of target (post-saccadic retinotopic persistence)		Distractor to left of target (pre-saccadic predictive remapping)	
	No. False-positives	Total trials	No. False-positives	Total trials
Pre-saccadic (200 to 0 ms before saccade offset)				
Subject JV	1	149	1	132
Subject JS	0	158	2	155
Subject LV	2	147	1	142
Subject MK	1	125	1	120
Total	4	579	5	549
Post-saccadic (0 to 150 ms after saccade offset)				
Subject JV	1	68	1	67
Subject JS	0	66	0	87
Subject LV	0	66	0	69
Subject MK	0	55	3	68
Total	1	255	4	291

Additional supplementary materials 1: Example eye traces



The example eye traces of trial No. 600-700 from subject BA in experiment 1 when he was performing the experiment and made a saccade in that trial. Not all of the trials showed here were included in further analysis (such as the one that the subject made a saccade before FP offset).The black and gray traces indicate the horizontal and vertical eye position respectively. In this experiment, the subject was asked to make a 7 visual angle degrees saccade to the right if he saw the fixation point jump. (the data from: mak-cha4s-bha-34567).

Additional supplementary materials 2: Subjects information and data files

Subject information

Three-letter code	Vision*	Age (years)	Gender	Handedness**
BHA	Corrected to normal	25	Male	Right handed
JEV	Normal	30	Female	Right handed
JUK	Normal	21	Female	Right handed
JIS	Corrected to normal	22	Female	Right handed
KAW	Corrected to normal	22	Male	Right handed
LEV	Normal	23	Female	Right handed
MAK	Normal	22	Female	Right handed
MSS	Normal	22	Male	Right handed
SNP	Corrected to Normal	26	Female	Right handed
TAO	Normal	29	Male	Right handed

Table 1: The basic information of the subjects participating into this study.

*: If the subjects wear glasses, their vision was 'corrected to normal'; otherwise, their vision was 'normal'.

**: The handedness defined here as the subjects use which hand to write.

Maclab data files

Note: In most of the cases, each file in the following pages was the data from one session, the length of each session could be different for each subjects. But, for some subjects, one subject could have less data files than others because the experimenter might only pause the experiment rather than terminated the experiment by exiting maclab when the subjects had a rest. The experimenter could also change the parameter after several sessions, which might cause the name of the first data file included in analysis with a larger numbers (such as LEV in experiment 1 and 2). The number in the data file names could be incontinuous because of the crash of maclab or other technical problems.

The first three letters in each data file name indicate the 3-letter code of the experimenter, follow the name of the epar running the experiment, then the 3-letter code of the subjects, then the number of the session.

Experiment 1

mak- cha4s -bha-003;
mak- cha4s -bha-004;
mak- cha4s -bha-005;
mak- cha4s -bha-006;
mak- cha4s -bha-007;
mak- cha4s -jev-001;
mak- cha4s -jev-002;
mak- cha4s -jev-003;
mak- cha4s -jev-004;
mak- cha4s -jev-005;
mak- cha4s -jev-006;
mak- cha4s -juk-001;
mak- cha4s -juk-002;
mak- cha4s -juk-003;
mak- cha4s -juk-004;
mak- cha4s -juk-005;
mak- cha4s -juk-006;
mak- cha4s -juk-007;
mak- cha4s -juk-008;
mak- cha4s -jis-005;
mak- cha4s - jis -006;
mak- cha4s - jis -007;
mak- cha4s - jis -008;
mak- cha4s - kaw -001;
mak- cha4s - kaw -002;
mak- cha4s - kaw -003;
mak- cha4s - kaw -004;
mak- cha4s - kaw -005;
mak- cha4s - kaw -006;
mak- cha4s - kaw -007;
mak- cha4s - lev -007;
mak- cha4s - lev -008;
mak- cha4s - lev -010;
mak- cha4s - lev -011;
mak- cha4s - lev -012;
mak- cha4s - lev -013;
mak- cha4s - mak -002;
mak- cha4s - snp -001;
mak- cha4s - snp -002;
mak- cha4s - snp -003;
mak- cha4s - snp -004;
mak- cha4s - snp -005;
mak- cha4s - snp -006;
mak- cha4s - snp -007;
mak- cha4s - snp -008;

Experiment 2

mak- attdif -jev-001;
mak- attdif -jev-003;
mak- attdif -jev-004;
mak- attdif -lev-004;
mak- attdif -lev-005;
mak- attdif -lev-006;
mak- attdif -lev-007;
mak- attdif -mak-001;
mak- attdif -mak-002;
mak- attdif - mss -001;
mak- attdif - mss -002;
mak- attdif - mss -003;
mak- attdif - mss -004;
mak- attdif - mss -005;
mak- attdif - mss -006;
mak-attdif-tao-0210;
mak-attdif-tao-0218;
mak-attdif-tao-0218-002;

Experiment 3

mak-cha6s-jev-002;
mak-cha6s-jis-002;
mak-cha6s-jis-003;
mak-cha6s-lev-001;
mak-cha6s-lev-002;
mak-cha6s-mak-001;

Additional supplementary materials 3: Consent form

09_02 Probandenaufklaerung-EN.pdf

Information for subjects participating in psychophysical tests in the Cognitive Neuroscience Laboratory, German Primate Center (DPZ)

Name of subject: _____

Project leader: _____

Cognitive Neuroscience Laboratory, DPZ

I. Subject requirements

Participation in the tests requires normal or corrected-to-normal vision, and unrestricted arm- and hand-mobility.

II. Aim of the study and benefit for the subject

You participate voluntarily in this study. The purpose of the study is an improved knowledge of human perception and behavior. With your participation you contribute to our understanding of brain functions, especially of perception, the planning of movement, and the role of selective attention. We investigate how the efficiency of the sensorimotor system is influenced by prior knowledge and by the exact sensory circumstances of a particular experimental situation. For example, your performance will be compared between tasks, which differ only in the focus of your visual attention. Differences in performance between these task conditions allow conclusions about the influence of selective attention to the processing of sensory information.

A detailed understanding of the function of the healthy organism and brain is an important prerequisite for helping patients suffering from specific visual or motor deficits. The participation in the tests per se does not yield any direct health benefit.

III. Design of the study

You will participate in measurements, in which we will test your sensory or sensorimotor performance. For this, a number of different stimuli will be presented in random order on a computer screen or with a tactile stimulator. You will sit on a chair in front of these devices, sometimes with your chin on a chin rest in order to guarantee a defined distance to the monitor. You will respond by pressing a button on a computer keyboard, by touching a touch-screen, by making an eye movement or by pressing a foot-switch (for simplicity we only speak of 'keystroke' in the following). A test consists of several trials. In each trial one or more visual stimuli will be presented. At the end of each trial you will respond with a keystroke. For example, the stimulus could consist of a moving pattern and you will have to decide if it is moving to the left or to the right. For some tests, it is important, that you change your direction of gaze as little as possible. For those tests, you will have to maintain your gaze on a small stimulus on the screen during the trials.

IV. Procedure

A single test normally consists of 50 to 200 trials of a few seconds duration each. A test will be finished after 5 to 20 minutes. During one session several tests and different tasks will be conducted. Before each new task you will have opportunity to practice. A session typically takes one hour, including breaks between the tests. You will set the pace as in most measurements you start every trial yourself and because you can take breaks whenever you choose. There are also breaks between the tests and the task of the next test will be explained. Typically, a study consists of several sessions and the first sessions are used for training. It is very important for us, that you finish a study completely. But

you are free to abort the measurements at any time.

V. Side effects

These tests are absolutely non-invasive experiments. There are no adverse effects. The computers and screens in use are standard equipment as used in offices and for computer games.

VI. Voluntariness of participation

The participation in the study is absolutely voluntary. You are entitled to quit the study at any time and without giving reasons.

VII. Payment

For the participation in the measurements you receive a payment. In some of our studies we investigate the influence of such payments on the performance of the subjects. In these sessions a basic payment is combined with an amount that depends on the psychophysical performance or is chosen at random.

VIII. Passing on of the data

The data collected in these studies will only be used or passed on anonymously.

Consent form:
I read and understood this information carefully. The experimenter answered all my questions. By signing this form I agree to

a) participate in the study and
b) to the publication of the collected data in an anonymous form.

I received a copy of this information sheet.

---------- ----------

Place and date Subject's signature

Cognitive Neuroscience Laboratory
German Primate Center – Leibniz Institute for Primate Research
Prof. Dr. Stefan Treue
Kellnerweg 4, 37077 Goettingen
Tel: 0551-3851-118

Vorsitzender des Aufsichtsrates: MR Dr. Axel Kollatschny;
Geschäftsführer: Prof. Dr. Stefan Treue, Assessor jur. Michael Lankeit;
Sitz der Gesellschaft: Göttingen; Handelsregister: Göttingen HRB 933

Additional supplementary materials 4:
Example epars & mpars

Note: The epars define the time sequence of the experiment, the location of the stimulus, i.e. when and where to show the stimulus on the screen. The epars also on-line control the data collection and some events related to subject performance (such as eye position, time window of reaction etc.). The mpars controls the properties of the stimuli, such as the motion direction, speed, dot density, color of the RDP.

Example epars:
Experiment 1
HuAtt4S.epar

```
projectLeader mak
expCode cha4s
displayWindowOnSecondMonitor 0 0 200 200
trialProtocol 1 7
0 000 1 0
1 0 0000
106 0 00 1 1
55   0  140  -160   1   0
55   0  140   160   1   0
55   0  140  -160   1   1
55   0  140   160   1   1
# 2 stimuli in FRF # 3 cue in FRF;
# 4 1st FP; 5 patch opposite to FRF; 6 cue for 5; 7
2nd FP or saccade target;
# 8 and 9 patches removed before saccade in FRF;
# 10 and 11 patches in RF; 12 and 13 patches
removed before saccade in RF.
# NOTE this epar is used to training only, 4
patches would change directions
displayCenter 0        1    0.4       0.5
displayCenter 1   1  280   0
filenames&pathname 7 :cha4sSlow:traceMpars:
Luminance.mpar
fixStim4.mpar
fixStim6.mpar
Att4TP.mpar
Att4DP.mpar
Att4DP1.mpar
Att4TPL.mpar
# 1 target + 3 distractors
# class 1, catch trials, no change for target, 3 times
less than other classes
# class 2, target in upper visual field, no change-
distractor.
# class3, target in upper visual field, change-
distractor in lower.
# class 4, target in upper visual field,change-
distractor in future RF.
classes 4
1 2 0 3 6 666 1 0 1
1 2 0 3 4 6 66 2 0 1
1 2 0 3 7 5 6 6 3 0 1
1 2 0 3 7 6 5 6 4 0 1
classFrequencyOption 2
classFrequency 2 3
classFrequency 3 3
classFrequency 4 3
keyboardResponse TRUE
allowedFinalResponseKeys 1 125
anticipatedResponseDuration 150
responseTimeWindow 600
fixpointIndexColor 255
backgroundIndexColor 100
fixPointSize 12
earlyResponsePermitted FALSE
fixPointVisibleBetweenTrials false
fixationRequired FALSE
collectEyePositions TRUE
fixAreaRadiusOfClass 0 80
smoothEyePositions 4
sampleSource 1
collectSpikes FALSE
numberOfTrials 9000
dotPosToBuffer FALSE
eyePosDecay -20
provideWords TRUE
openDataFile
savePupilDiameter TRUE
minPhaseChangeDistance 34
evaHack TRUE
leverDownRewardDuration 0
leverReleaseDuration 600
```

Example mpars:

Luminance.mpar

```
numberOfSurfaces        1       0       0
pixelradius     8
numberOfFrames          300
qtRGBForeColor 65000    65000   65000
qtSquare        -6      -6      6       6
changePhase     -150    250
qtRGBForeColor 35000    35000   35000
qtSquare        -6      -6      6       6
changePhase     10      10
qtRGBForeColor 65000    65000   65000
qtSquare        -6      -6      6       6
```

FixStim4.mpar
numberOfSurfaces 1 40 0
pixelradius 10
numberOfFrames 105
#qtRGBForeColor 6553 6553 0
qtIndexForeColor 255
qtSquare -6 -6 6 6
qtSuspendFix 103 152
qtFixFactor 105 -1 1.5
qtFixDispCtr 105 -1 1

Fixstim6.mpar
numberOfSurfaces 1 40 0
pixelradius 10
numberOfFrames 200
#qtRGBForeColor 6553 6553 0
qtIndexForeColor 255
qtSquare -6 -6 6 6
qtSuspendFix 103 152
qtFixFactor 105 -1 1.5
qtFixDispCtr 105 -1 1

Att4TP.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 4
shape circle
colorIndex 255
direction 0
changePhase -20 100
directionTable 2 90 270
speed 32
changePhase 2 2
direction 0
speed 4

Att4DP.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 4
shape circle
colorIndex 255
direction 0
changePhase 10 160
directionTable 2 90 270
speed 32
changePhase 2 2
direction 0
speed 4

Att4DP1.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 4
shape circle
colorIndex 255
direction 0

Att4TPL.mpar
[numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 4
shape circle
colorIndex 255
direction 0
changePhase -10 160
directionTable 2 90 270
speed 32
changePhase 2 2
direction 0
speed 4

Experiment 2

Attdif.epar

projectLeader mak
expCode AttDif
displayWindowOnSecondMonitor 0 0 200 200
trialProtocol 1 7
0 000 1 0
1 0 00 1 0
106 0 00 1 1
35 0 140 -160 1 0
35 0 140 160 1 0
35 0 140 -160 1 1
35 0 140 160 1 1
2 stimuli in FRF # 3 cue in FRF;
4 1st FP; 5 patch opposite to FRF; 6 cue for 5; 7 2nd FP or saccade target;
8 and 9 patches removed before saccade in FRF;
10 and 11 patches in RF; 12 and 13 patches removed before saccade in RF.
NOTE this epar is used to training only, 4 patches would change directions
displayCenter 0 1 0.4 0.5
displayCenter 1 1 280 0
filenames&pathname 13 :AttDiff:traceMpars:
Luminance.mpar
fixStim4.mpar
fixStim6.mpar

Att4TP.mpar
Att4DP.mpar
Att4DP1.mpar
Att4TPL.mpar
Att4TP40.mpar
Att4DP40.mpar
Att4TPL40.mpar
Att4TP55.mpar
Att4DP55.mpar
Att4TPL55.mpar
1 target + 3 distractors
class 1, catch trials, no change for target, 3 times less than other classes
class 2,5, target in upper visual field, no change-distractor.
class 3,6, target in upper visual field.change-distractor in lower.
class 4,7, target in upper visual field,change-distractor in future RF.

classes 7
1 2 0 3 6 666 1 0 1
1 2 0 3 8 6 66 2 0 1
1 2 0 3 10 9 6 6 3 0 1
1 2 0 3 10 6 9 6 4 0 1
1 2 0 3 11 6 66 5 0 1
1 2 0 3 13 12 6 66 0 1
1 2 0 3 13 6 12 6 7 0 1
classFrequencyOption 2
classFrequency 5 4
classFrequency 2 4
classFrequency 3 2
classFrequency 4 2
classFrequency 6 2
classFrequency 7 2

keyboardResponse TRUE
allowedFinalResponseKeys 1 125
anticipatedResponseDuration 150
responseTimeWindow 600
fixpointIndexColor 255
backgroundIndexColor 100
fixPointSize 12
earlyResponsePermitted FALSE
fixPointVisibleBetweenTrials FALSE
fixationRequired FALSE
collectEyePositions TRUE
fixAreaRadiusOfClass 0 80
smoothEyePositions 4
sampleSource 1
collectSpikes FALSE
numberOfTrials 9000
dotPosToBuffer FALSE
eyePosDecay -20
provideWords TRUE
openDataFile
savePupilDiameter TRUE
minPhaseChangeDistance 34
evaHack TRUE
leverDownRewardDuration 0
leverReleaseDuration 600

Example mpars:

Att4TP40.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 8
shape circle
colorIndex 255
direction 0
changePhase -50 110
directionTable 2 40 320
changePhase 2 2
direction 0
speed 8

Att4DP40.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 8
shape circle
colorIndex 255
direction 0
changePhase 10 160
directionTable 2 40 320
changePhase 2 2
direction 0
speed 8

Att4TPL40.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 8
shape circle
colorIndex 255
direction 0
changePhase -20 140
directionTable 2 40 320
changePhase 2 2
direction 0
speed 8

Experiment 3

Cha6S.epar

```
projectLeader mak
expCode cha6s
displayWindowOnSecondMonitor 0 0 200 200
trialProtocol 1 9
0 0 0 0 1 0
1 0 0 0 0 0
106 0 0 0 1 1
55   0  140  -160   1   0
55   0  140   160   1   0
55   0  140  -160   1   1
55   0  140   160   1   1
55   0  -140  -160  1   0
55   0  -140   160  1   0
# 2 stimuli in FRF # 3 cue in FRF;
# 4 1st FP; 5 patch opposite to FRF; 6 cue for 5; 7
2nd FP or saccade target;
# 8 and 9 patches removed before saccade in FRF;
# 10 and 11 patches in RF; 12 and 13 patches
removed before saccade in RF.
# NOTE this epar is used to training only, 4
patches would change directions
displayCenter 0         1    0.4        0.5
displayCenter 1         1    280        0
filenames&pathname 9 :cha6sSlow:traceMpars:
Luminance.mpar
fixStim4.mpar
fixStim6.mpar
Att4TP.mpar
Att4DP.mpar
Att4DP1.mpar
Att4TPL.mpar
Att4TPL2.mpar
Att4TPL0.mpar
# 1 target + 5 distractors
# class 1, catch trials, no change for target, 3 times
less than other classes
# class 2, target in upper visual field, no change-
distractor.
# class 3, target in upper visual field.change-
distractor in left (remapping location).
# class 4, target in upper visual field,change-
distractor in future RF.
classes 4
1 2 0 3 9 6 6 6 6 6 1 0 1
1 2 0 3 4 6 6 6 6 6 2 0 1
1 2 0 3 7 6 6 6 5 6 3 0 1
1 2 0 3 7 6 5 6 6 6 4 0 1
classFrequencyOption 2
classFrequency 2 5
classFrequency 3 4
classFrequency 4 4
keyboardResponse TRUE
allowedFinalResponseKeys 1 125
anticipatedResponseDuration 150
responseTimeWindow 600
fixpointIndexColor 255
backgroundIndexColor 100
fixPointSize 12
earlyResponsePermitted FALSE
fixPointVisibleBetweenTrials false
fixationRequired FALSE
collectEyePositions TRUE
fixAreaRadiusOfClass 0 80
smoothEyePositions 4
sampleSource 1
collectSpikes FALSE
numberOfTrials 9000
dotPosToBuffer FALSE
eyePosDecay -20
provideWords TRUE
openDataFile
savePupilDiameter TRUE
minPhaseChangeDistance 34
evaHack TRUE
leverDownRewardDuration 0
leverReleaseDuration 600
```

Example mpars:

fixStim4.mpar

```
numberOfSurfaces 1 40 0
pixelradius        10
numberOfFrames 105
#qtRGBForeColor          6553 6553 0
qtIndexForeColor 255
qtSquare          -6        -6        6          6
qtSuspendFix     103 152
qtFixFactor                105 -1   1.5
qtFixDispCtr      105 -1   1
```

fixStim6.mpar

```
numberOfSurfaces 1 40 0
pixelradius        10
numberOfFrames 200
qtIndexForeColor 255
qtSquare          -6        -6        6          6
qtSuspendFix     103 152
qtFixFactor                105 -1   1.5
qtFixDispCtr      105 -1   1
```

Att4TP.mpar

```
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 4
shape circle
colorIndex 255
```

direction 0
changePhase -35 75
directionTable 2 90 270
speed 32
changePhase 2 2
direction 0
speed 4

Att4DP.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 4
shape circle
colorIndex 255
direction 0
changePhase 40 80
directionTable 2 90 270
speed 32
changePhase 2 2
direction 0
speed 4

Att4DP1.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 250
speed 4
shape circle
colorIndex 255
direction 0

Att4TPL.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 300
speed 4
shape circle
colorIndex 255
direction 0
changePhase -75 185
directionTable 2 90 270
speed 32
changePhase 2 2
direction 0
speed 4

Att4TPL0.mpar
numberOfSurfaces 1 40 10
dotSize 6
pixelradius 80
numberOfFrames 300
speed 4
shape circle
colorIndex 255
direction 0
changePhase -40 185
directionTable 2 0 0
changePhase 2 2
direction 0
speed 4

Chapter 4

An attention-sensitive memory trace in macaque MT following saccadic eye movements

PLOS | BIOLOGY

RESEARCH ARTICLE

An Attention-Sensitive Memory Trace in Macaque MT Following Saccadic Eye Movements

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Abstract

We experience a visually stable world despite frequent retinal image displacements induced by eye, head, and body movements. The neural mechanisms underlying this remain unclear. One mechanism that may contribute is transsaccadic remapping, in which the responses of some neurons in various attentional, oculomotor, and visual brain areas appear to anticipate the consequences of saccades. The functional role of transsaccadic remapping is actively debated, and many of its key properties remain unknown. Here, recording from two monkeys trained to make a saccade while directing attention to one of two spatial locations, we show that neurons in the middle temporal area (MT), a key locus in the motion-processing pathway of humans and macaques, show a form of transsaccadic remapping called a memory trace. The memory trace in MT neurons is enhanced by the allocation of top-down spatial attention. Our data provide the first demonstration, to our knowledge, of the influence of top-down attention on the memory trace anywhere in the brain. We find evidence only for a small and transient effect of motion direction on the memory trace (and in only one of two monkeys), arguing against a role for MT in the theoretically critical yet empirically contentious phenomenon of spatiotopic feature-comparison and adaptation transfer across saccades. Our data support the hypothesis that transsaccadic remapping represents the shift of attentional pointers in a retinotopic map, so that relevant locations can be tracked and rapidly processed across saccades. Our results resolve important issues concerning the perisaccadic representation of visual stimuli in the dorsal stream and demonstrate a significant role for top-down attention in modulating this representation.

Author Summary

Humans experience a visually stable world despite the fact that eye, head, and body movements cause frequent shifts of the image on the retina. Humans and monkeys are also able to keep track of visual stimuli across such movements. One mechanism that may contribute to these abilities is "transsaccadic remapping," in which the responses of some neurons

Competing Interests: The authors have declared that no competing interests exist.

Abbreviations: FEF, frontal eye field; LIP, lateral intraparietal area; MST, medial superior temporal area; MT, middle temporal area; PSTH, peristimulus time histogram; RDP, random dot pattern; RF, receptive field; SC, superior colliculus.

in various attentional, oculomotor, and visual brain areas appear to anticipate the consequences of saccades. A current hypothesis proposes that the brain maintains "attentional pointers" to the locations of relevant stimuli and that, via transsaccadic remapping, it rapidly relocates these pointers to compensate for intervening eye movements. Whether stimulus features are also remapped across saccades (along with their location) remains unclear. Here, we show the presence of transsaccadic remapping in a macaque monkey brain area critical for visual motion processing, the middle temporal area (MT). This remapped response is stronger for an attended stimulus. We find only weak evidence for motion-direction information in the remapped response. These results support the attentional pointer hypothesis and demonstrate for the first time, to our knowledge, the impact of top-down attention on transsaccadic remapping in the brain.

Introduction

Prior research has revealed the potential contribution to visual processing of transsaccadic remapping, in which some neurons in the lateral intraparietal area (LIP), frontal eye field (FEF), superior colliculus (SC), medial superior temporal area (MST), and ventral stream (areas V3a, V3, and V2) respond perisaccadically as long as a visual stimulus could be anticipated in their receptive fields (RFs) after the saccade [1–7]. This "remapped response" is not a simple visual afferent response, because it appears even when the visual stimulus disappears just before the saccade (that would bring the stimulus location into the RF), so that no stimulus ever appears in the neurons' visual RF before or after the saccade. Furthermore, in some neurons, it begins with a latency shorter than the normal visual latency and can even begin before saccade onset, in which case it has been referred to as "predictive remapping" [1]. More commonly, the remapped response occurs postsaccadically, and when this occurs in a situation in which there is no postsaccadic stimulus in the RF because it disappeared before the saccade, the remapped response is referred to as a "memory trace" of the location of the visual stimulus [1].

The functional role of this remapped response is currently being actively debated, and many of its key response properties remain unknown. It has been proposed [8] that transsaccadic remapping represents the predictive, presaccadic shift of attentional pointers on a retinotopic map that keeps track of attended locations across saccades, so that attended locations can be preferentially processed with minimal delay after the saccade. This reduction of delay would be especially helpful when planning rapid sequential saccades and could also help maintain an uninterrupted visual experience across saccades. Others have suggested that this view may be too restrictive and that information about visual features are also remapped across saccades, in addition to location [9–12]. This alternative view thus invokes an additional role for transsaccadic remapping in spatiotopic feature comparison and adaptation transfer across saccades. Resolving these issues requires a better understanding of the properties of the remapped response in different brain areas. Here, we address and answer several open questions regarding the remapped response in the middle temporal area (MT), a key motion processing area, in the rhesus macaque.

MT is an important locus in the processing of visual motion and is strongly interconnected with LIP, FEF, SC, and MST. A previous report from macaque MT showed the absence of predictive remapping [13] in MT neurons; our results are consistent with this. Another recent report reported the presence of a memory trace in MST neurons but failed to find a memory trace in a small sample of MT neurons using a paradigm with a flashed visual stimulus; the

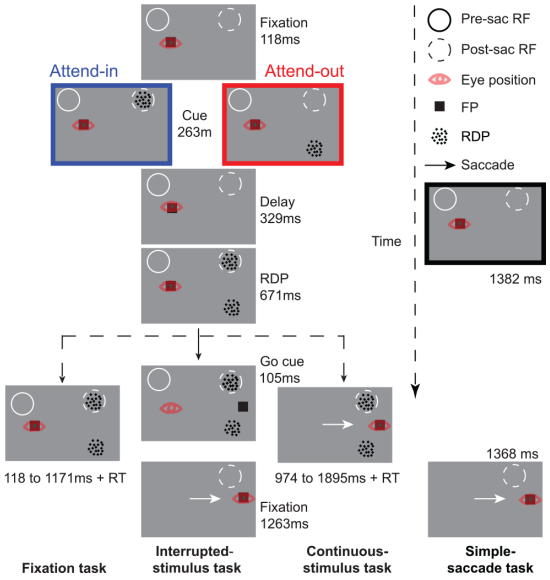

Fig 1. Task design and timing. Two rhesus monkeys were trained to perform a task that involved attending to one of two moving RDPs while also making a visually guided saccade if the fixation point jumped to a new location (continuous-stimulus task and fixation task). On about 44% of trials, the RDPs disappeared just before the saccade (interrupted-stimulus task). On about 11% of trials, RDPs were never presented and the monkey only had to make a visually guided saccade (simple-saccade task). Values next to each panel represent the durations of the task phase represented by that panel. For details, see Materials and Methods and S1 Text.

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authors therefore suggested that the memory trace may be an emergent property that differentiates MST from MT [2]. Here, we report that MT neurons do show a memory trace, using an experimental paradigm that requires the monkey to pay top-down attention to one of two motion stimuli. Furthermore, we show that the memory trace in MT neurons is enhanced by top-down spatial attention. This is the first demonstration, to our knowledge, of the influence of top-down attention on the memory trace in any brain area. Finally, we find evidence only for a weak and transient effect of motion direction on the memory trace in one monkey. Our data are therefore consistent with the hypothesis that transsaccadic remapping represents the shift of attentional pointers in a retinotopic map. Our results further clarify the perisaccadic representation of visual stimuli in the dorsal stream and demonstrate a significant role for top-down attention in modulating this representation.

Results

We report the responses of 90 MT neurons, 46 from monkey H and 44 from monkey E. We first considered the responses from 0 to 500 ms after saccade offset (see Methods) in the continuous-stimulus task (Fig 1), in which the monkeys made a saccade that brought either the (previously cued) target random dot pattern (RDP) or the distractor RDP into their RF, and no stimulus was present in the RF before the saccade. As previously reported (e.g., [14–16]), neurons showed a clear postsaccadic enhancement for attended (solid blue curves, Fig 2A and 2B) versus unattended (dotted red curves, Fig 2A and 2B) RDPs moving in the preferred direction in their RF. Compared to the distractor RDP, the response to the (cued) target RDP moving in

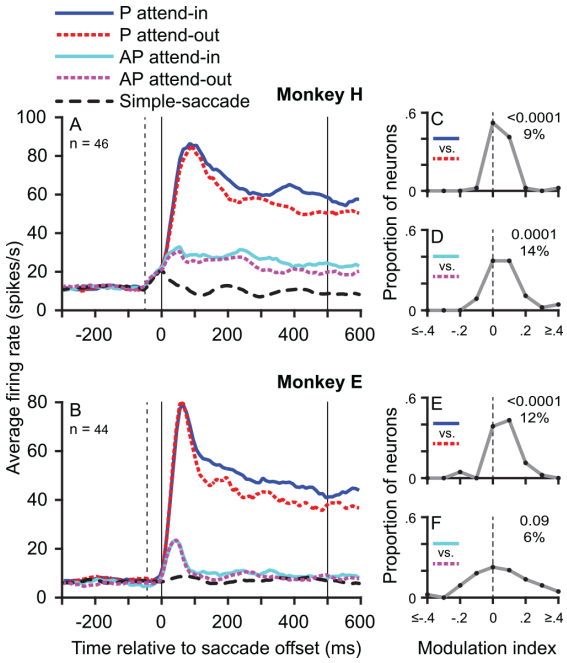

Fig 2. Attentional enhancement of MT neuronal responses to moving RDPs. (A,B) Population average peristimulus time histograms (PSTHs) for monkey H (A) and monkey E (B) in response to attended (target) and unattended (distractor) RDPs moving either in the preferred (P) or antipreferred (AP) direction (see legend at top left). The PSTH for the simple-saccade task is also shown in black as a reference. Solid vertical lines demarcate the time window used for computing the modulation indices in C–F. The dotted vertical line indicates the mean time of saccade onset. (C,E) Frequency polygons of the distribution of modulation indices in monkey H (C) and monkey E (E) when the preferred direction RDP is in the RF after the saccade show a clear predominance of values greater than zero, i.e., an enhanced response in the attend-in conditions. The *p*-value from the signed-rank test of the modulation indices and the median modulation index (converted to a percentage and rounded) are shown on the top right of each panel. The final point in the frequency polygons sums all data values at or beyond the extreme value. (D,F) Same as C,E but for the antipreferred direction RDP. Data in Supporting Information (S1 Data).

doi:10.1371/journal.pbio.1002390.g002

the preferred direction in a time window of 0 to 500 ms following saccade offset was greater by a median value of 8.9% in monkey H (Fig 2C, $p < 0.0001$) and 12.4% in monkey E (Fig 2E, $p < 0.0001$). The attentional modulation of an antipreferred direction target was significant in monkey H (Fig 2D, 13.7%, $p = 0.0001$) but not in monkey E (Fig 2F, 5.8%, $p = 0.0909$). Consistent with a prior report [13], we observed no predictive remapping, i.e., no presaccadic increase in activity in MT neuronal responses (Figs 2A, 2B and S1).

MT Neurons Show a Memory Trace That Is Enhanced by Top-Down Attention

In contrast to the continuous-stimulus task above, the RDPs in the interrupted-stimulus task (Fig 1) disappear before saccade onset. Thus, a neuronal response after the saccade would represent a memory trace and not a sensory response, since there is no stimulus in the postsaccadic RF (or in the presaccadic RF). To determine the presence of a memory trace, we considered the responses in the interrupted-stimulus task when the target RDP (irrespective of motion direction) was at the postsaccadic RF location before the saccade (attend-in interrupted-

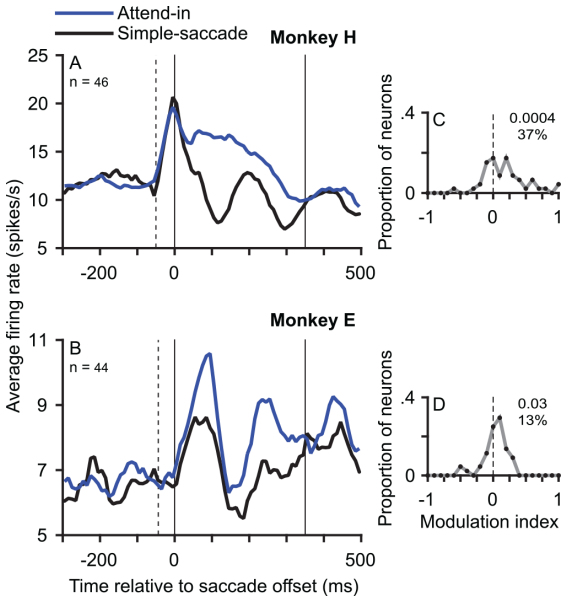

Fig 3. MT neurons show a memory trace. The memory trace is an enhanced postsaccadic response (compared to the simple-saccade) when a moving target RDP was presented (only before the saccade) at their postsaccadic RF location. We pooled the responses to the two RDP directions because we did not find an influence of RDP motion direction on the memory trace (Fig 5). (A,B) Population average PSTHs for monkey H (A) and monkey E (B) in the attend-in condition of the interrupted-stimulus task (blue) compared to the simple-saccade task (black). The *y*-axes in A and B have different ranges. (C,D) Frequency polygons of the distribution of modulation indices (for the response from 0 to 350 ms after saccade offset) comparing these two conditions in monkey H (C) and monkey E (D) show a clear predominance of values greater than zero, i.e., an enhanced response in the attend-in condition. Conventions as in Fig 2. Data in Supporting Information (S2 Data).

doi:10.1371/journal.pbio.1002390.g003

stimulus condition). We compared this response from 0 to 350 ms after saccade offset (see Methods) to the response in the same time window in the simple-saccade task where the monkey only made a saccade with no RDP ever appearing on the screen (Fig 3). We found a strong enhancement of responses in the attend-in condition of the interrupted-stimulus task compared to the simple-saccade task (Fig 3A and 3B, blue curve versus black curve), and we interpret this enhancement as a memory trace of the visual stimulus presented before the saccade. The median enhancement of the response following saccade offset in the attend-in interrupted-stimulus condition was 37.4% ($p = 0.0004$) in monkey H and 13.1% ($p = 0.0308$) in monkey E.

In order to examine the effect of attention on the memory trace, we then compared the memory trace for the target (in the attend-in interrupted-stimulus condition) to that for the distractor RDP (in the attend-out interrupted-stimulus condition): in both cases, the RDP was in the postsaccadic RF before the saccade but not after it. The memory trace for the target was clearly greater than that for the distractor RDP (Fig 4A and 4B, blue curve versus red curve). The median enhancement of the memory trace for the target relative to that for the distractor was 25.4% ($p < 0.0001$, Fig 4C) in monkey H and 14.1% ($p = 0.0022$, Fig 4E) in monkey E. The memory trace for the distractor, on the other hand, was either weak or absent. Based on the modulation indices, the memory trace for the distractor was not significantly different from when there was no stimulus in the simple-saccade condition (Fig 4A and 4B, red curve

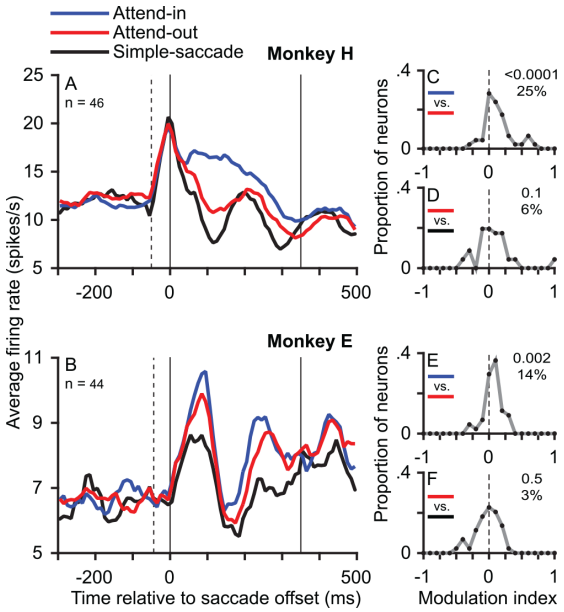

Fig 4. The memory trace is sensitive to top-down attention. The postsaccadic response is larger when a target RDP (as compared to a distractor RDP) was in the postsaccadic RF location before the saccade. (A,B) Population average PSTHs for monkey H (A) and monkey E (B) in the attend-in condition (blue) and attend-out condition (red) of the interrupted-stimulus task, pooled across motion directions as well as the simple-saccade task (black). The *y*-axes in A and B have different ranges. (C,E) Frequency polygons of the distribution of modulation indices comparing the attend-in and attend-out conditions in monkey H (C) and monkey E (E) show a clear predominance of values greater than zero, i.e., an enhanced response in the attend-in condition. (D,F) Frequency polygons of the distribution of modulation indices comparing the attend-out condition of the interrupted-stimulus task and the simple-saccade task in monkey H (D) and monkey E (F) show no significant difference in the responses. Conventions as in Figs 2 and 3. Data in Supporting Information (S3 Data).

doi:10.1371/journal.pbio.1002390.g004

compared to black curve): the response in the attend-out condition was larger by 6.4% ($p = 0.1417$, Fig 4D) in monkey H and by 2.7% ($p = 0.5222$, Fig 4F) in monkey E. However, this lack of significance appears to contrast with the effect that is visible in the average population PSTHs (red versus black curves in Fig 4A and 4B). This is because the separation between the average population PSTHs reflects the difference between the mean firing rates in the two conditions, while the median modulation index is a measure based on the ratio of firing rates. Performing a paired *t* test between the firing rates in the attend-out and simple-saccade condition does reveal a significant enhancement in the attend-out condition (Monkey H: mean difference = 1.3 spikes per second, $p = 0.0450$; Monkey E: mean difference = 0.8 spikes per second, $p = 0.0270$).

The MT Memory Trace Only Shows a Transient Effect of Motion Direction (In One Monkey)

We examined whether the attention-sensitive memory trace in MT also contains information about the motion direction of the stimulus that elicited the memory trace, whether it be the target or the distractor RDP. We calculated the responses for trials in which the preferred or anti-preferred direction RDP (as identified from the continuous-stimulus task) was in the

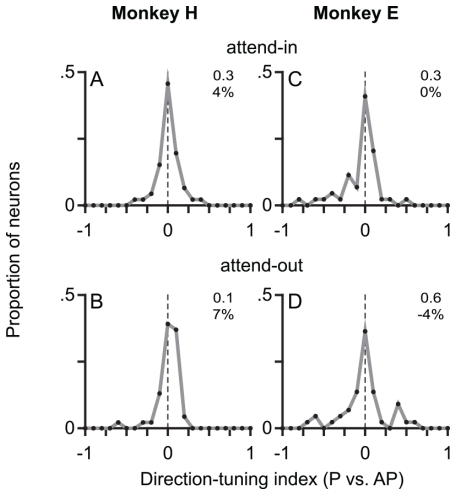

Fig 5. The memory trace (from 0 to 350 ms) is not sensitive to motion direction. The postsaccadic response is not significantly different when the preferred (P) or antipreferred (AP) direction RDP was in the postsaccadic RF location before the saccade. The four panels show frequency polygons of the distribution of direction-tuning indices (see Methods) for the attend-in (A,C) and attend-out (B,D) conditions of the interrupted-stimulus task (for the response from 0 to 350 ms after saccade offset). Results for monkey H in the left column (A,B) and for monkey E in the right column (C,D). None of the distributions show a statistically significant deviation from zero. Preferred and antipreferred directions were defined based on the response in the continuous-stimulus task. Other conventions as in Figs 2–4. Data in Supporting Information (S4 Data).

doi:10.1371/journal.pbio.1002390.g005

postsaccadic RF. We did not find any significant effect of motion direction when we compared the responses in either the attend-in condition (with the target RDP in the postsaccadic RF location) or the attend-out condition (with the distractor RDP in the postsaccadic RF location). None of the response differences (Fig 5A–5D) were statistically significant (all p-values > 0.1248). Additionally, since the preferred and antipreferred directions defined on the basis of the responses in the continuous-stimulus task may not predict the memory trace in the interrupted-stimulus task, we used a two-fold approach. We first computed the response after saccade offset on even-numbered trials and designated the motion direction that elicited the larger response as the preferred direction. We then used odd-numbered trials to perform the same analysis of the effects of motion direction on the memory trace. Once again, none of the response differences were statistically significant (all p-values > 0.1292).

Since it is possible that motion-direction selectivity may be present in the memory trace at shorter time scales, we also examined the motion-direction selectivity of the memory trace over shorter time periods (Fig 6). There was no evidence for motion-direction selectivity in the memory trace for monkey H in either the attend-in (Fig 6A and 6E) or the attend-out (Fig 6B and 6F) conditions, as evidenced by the fact that the 95% confidence bands (Fig 6E and 6F) included zero throughout the time course and none of the nonoverlapping statistical comparisons (Bonferroni-corrected for multiple comparisons) were statistically significant. The results from monkey E were similar, except that there was a transient effect of motion direction on the memory trace (Fig 6C and 6G) in the attend-in condition, where the memory trace for the nonpreferred direction was larger in the time window from 50 to 100 ms after saccade offset ($p = 0.0031$ for the direction-tuning index and 0.0024 for the difference in firing rates). Examining the response in this time window in each individual neuron (using a rank-sum test comparing the responses to the preferred and nonpreferred directions) did not yield significance

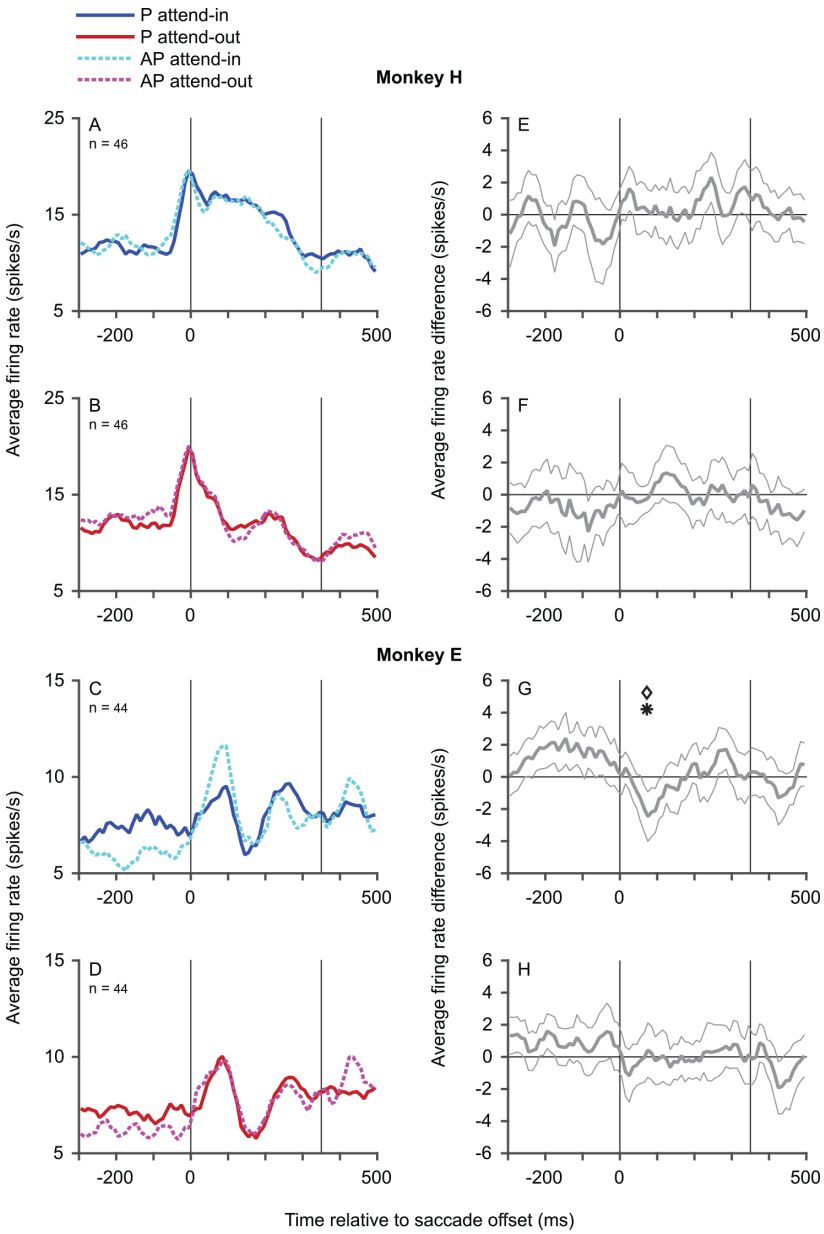

Fig 6. Evidence only for transient feature-related information in the memory trace in one monkey. In the left column, population average PSTHs for the preferred direction (blue trace in A,C and red trace in B,D) and nonpreferred direction (cyan trace in A,C and magenta trace in B,D) for the attend-in (A,C) and attend-out (B,D) conditions of the interrupted-stimulus task are plotted. Preferred and nonpreferred directions were determined from the responses in the continuous-stimulus task. In the right column, the mean difference (averaged across neurons) between the PSTH for the preferred and nonpreferred direction is plotted (along with the 95% confidence bands) for the attend-in (E,G) and attend-out (F,H) conditions. All PSTHs calculated using overlapping 50 ms bins, stepping every 10 ms. Data from monkey H (A–B,E–F) and monkey E (C–D, G–H). Statistical significance was calculated (using signed-rank tests Bonferroni-corrected for 16 comparisons) using the difference between firing rates (diamond symbols) as well as using the modulation

index (asterisk symbol) in nonoverlapping 50 ms windows over the entire analysis period (16 comparisons over 800 ms from -300 to 500 ms relative to saccade offset). Only one time bin (G) showed significance. Other conventions as in Fig 2. Data in Supporting Information (S5 Data).

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for any neuron. Also, using a more liberal false-discovery rate correction for multiple comparisons did not change the result for the post-saccadic time bins, but indicated a significant effect of motion direction before the saccade (as suggested by the PSTHs in Fig 6C, with the responses in the blue trace being slightly larger than the cyan trace). These presaccadic effects could reflect weak stimulus-driven effects from outside the RF [17] and/or the effects of feature-based attention [18].

In both monkeys, a transient increase in activity that starts either before or immediately after saccade offset is visible in the average population PSTHs from all three tasks: the simple-saccade task, the interrupted-stimulus task (Fig 4A and 4B), and the continuous-stimulus task (Fig 2A and 2B). For the simple-saccade task, similar responses have been reported before, with substantial variability in individual neurons ([19,20]; also see Discussion). The apparent difference in time course in this response between the two monkeys may represent differences in the sampled population of neurons, since a subset of neurons (with more eccentric RFs) from monkey E shows a time course quite similar to that in monkey H. The genesis and properties of this response difference, though not fully understood, are beyond the focus of this paper, since our experiment was not designed to study it.

Discussion

We report that MT neurons show a memory trace: they respond more strongly after a saccade when a stimulus is present only before the saccade in their postsaccadic RF location. Furthermore, we show that the memory trace is stronger for an attended stimulus and does not contain information about motion direction. A memory trace has been shown previously in areas like LIP, FEF, SC, and MST [1–3,5,6], with which MT is strongly anatomically connected [21–23]. Another recent study by Inaba and Kawano [2] reported that a sample of 46 MT neurons did not carry information about the location of a recently disappeared stimulus in their postsaccadic response; they only found such information in the responses of MST neurons and concluded that the memory trace was an emergent property of MST neurons. Our task differs from theirs because it required the monkey to pay (top-down) attention to one of two stimuli, while their task only required the monkey to make a simple, visually guided saccade and the stimulus used to probe the memory trace was task-irrelevant. The difference between our results might therefore be partially explained by our result that MT neurons show a clear memory trace for attended stimuli, with the memory trace for unattended stimuli being weak or absent. However, other aspects might also contribute. First, the two studies probably sampled different kinds of neurons: the study by Inaba and Kawano excluded neurons that showed a response in the simple-saccade task, while the neurons in our sample show a transient response in the simple-saccade task (Fig 3). Such a transient response has been reported before from area MST [19] as well as area MT, even following saccades made in the dark (Ibbotson, M.R., personal communication, even though an earlier report from Ibbotson and colleagues [24] reported the absence of such a response in a small sample of 17 MT neurons). Further supporting the possibility that different neurons were sampled, the study by Inaba and Kawano reported that MT neurons showed a substantially longer latency (relative to saccade offset) to stimuli brought into their RFs by a saccade compared to stimuli flashed in their RF. This differs from the conclusion reached by another recent study [13] in which no difference was found between the two latencies. Though we do not present an analysis of response latency here, the

average population PSTHs (Fig 2A and 2B) suggest that the average latency is not longer than that expected from previous reports on MT neurons (between 30 and 40 ms [2,13]). Second, the polarity of the stimuli used was also different: the study by Inaba and Kawano used a white stimulus on a dark background, while we used a dark stimulus on a white background, and such polarity differences are known to have strong effects on the responses of V1 neurons [25]. Finally, the study by Inaba and Kawano relied on a receiver operating characteristic analysis performed within a sliding 10 ms window to report the absence of spatial tuning in the postsaccadic response 0 to 100 ms after saccade offset. Based on our results, it is possible that the 10 ms window may be too narrow and the 100 ms window too short to reliably detect tuning.

We show that the memory trace in MT neurons is larger for an attended stimulus; this is the first demonstration of the influence of top-down attention on the memory trace in any brain area. The task required the monkey to attend to the stimulus location throughout the trial. This stimulus location lay outside the recorded neuron's RF before the saccade and inside it only after the saccade. Therefore, assuming a single locus of attention, the monkey would have to shift attention from its presaccadic location on a retinotopic map (outside the RF) to its postsaccadic location (inside the RF) right around the saccade. It is also possible that two loci of attention simultaneously exist and that, around the saccade, attention is allocated simultaneously to both task-relevant locations (the presaccadic and postsaccadic stimulus locations on the retinotopic map). Previous psychophysical data from humans indicate that attentional effects are visible at the postsaccadic retinotopic location of a task-relevant stimulus shortly before saccade onset [26–28]. In our task, the neural data from MT indicate that attentional effects emerge in MT soon after saccade offset, but not before that (Figs 2 and S2). Based on our results, we suggest that the memory trace can be explained as the postsaccadic enhancing effect of a perisaccadic allocation of attention to the RF location (on a retinotopic map), where the monkey expects the target to be. Since there is no longer a stimulus in the neuron's RF, attention acts on the baseline, stimulus-independent activity to produce the memory trace. Psychophysically, attentional effects may have been visible in our task either before the saccade (though MT only shows postsaccadic attentional effects) or after the saccade (around the same time as the emergence of attentional effects in MT); since our task design did not allow us to measure the dynamics of attention psychophysically, we cannot distinguish between these two possibilities. Our interpretation of the memory trace as reflecting a top-down attentional effect in our task is consistent with previous findings showing stronger remapped responses for salient or task-relevant stimuli: LIP neurons show stronger levels of anticipatory (predictive) remapping to the appearance of a visual search target [29] or saccade target [30] in their RF after a saccade, compared to the appearance of a distractor. Similarly, stimuli with greater bottom-up saliency have been shown to elicit stronger remapped responses in LIP [30] and FEF [31]. When using a measure based on the difference of spike rates, our data indicate a weak memory trace for the unattended stimulus. However, this effect is not present when using a measure based on the ratio of spike rates. More data with a greater number of stimuli are needed before reaching more general conclusions about the extent to which unattended stimuli are also transsaccadically remapped.

The phenomenology of presaccadic remapping of visual RFs measured using flashed stimuli is currently controversial. The classical position in the literature is that neurons that show predictive remapping in LIP [1], FEF [4], and SC [6] are anticipating the appearance of a stimulus in their postsaccadic RF (as if they are shifting their RFs preemptively to their future postsaccadic locations). In contrast, it has recently been proposed [32,33], based on recordings from FEF, that such remapping actually represents a transient shift of visual RFs toward the saccade target and that this transient shift is correlated with the attentional shift to the saccade target before the saccade [34,35]. While these two views await reconciliation, we emphasize that our

experimental design and interpretation of the memory trace in MT is not dependent on either of these competing accounts of the phenomenology of predictive visual RF shifts measured using flashed stimuli. Our design and interpretation instead depend only on the fairly large body of evidence supporting spatially accurate remapping: psychophysical evidence from double-step experiments [36], free-viewing visual search [37], and transsaccadic attentional measurements [15,27] all show that the locations of salient stimuli and future saccade targets are remapped rapidly and accurately across saccades. Similarly, LIP [29,30] and FEF [38] neurons anticipatorily signal the presence of a target in their RFs. SC, LIP, and FEF neurons signal the location of the impending second saccade within their RFs in a double-step task [39–42]. SC neurons also rapidly compensate for midsaccade deviations in eye position introduced by electrical stimulation in the SC during a saccade [43,44]. The relationship of this spatially accurate remapping mechanism to the contentious spatial properties of predictive visual RF shifts is unclear at present.

The presence of feature-related information in the remapped response has become a critical test that distinguishes between two alternative views of the functional role of transsaccadic remapping that are being actively debated [8,9,11,32,45]. Absence of featural information in the remapped response would support the proposal [8] that transsaccadic remapping represents the predictive, presaccadic shift of attentional pointers on a retinotopic map that keeps track of attended locations across saccades. On the other hand, the presence of featural information in the remapped response would support the proposal that transsaccadic remapping plays an additional role in spatiotopic feature comparison and adaptation transfer across saccades [9–12], though the data on adaptation transfer have not been universally replicated (summarized in [46]). Our data clearly indicate that any motion-direction information present in the remapped response is weak: in our data, it was only present transiently in one monkey. This, combined with the greater memory trace elicited by the attended stimulus, indicates that the memory trace in MT neurons predominantly represents the effects of a shift of attentional pointers. We note here that evidence for featural information in the remapped response has been presented recently from LIP [47], and neurons that signal transsaccadic changes in stimulus location and/or color in their postsaccadic reafferent response have been found in FEF (though its relationship to remapping is unclear [12]). However, these areas only show coarse tuning to stimulus features, and our data provide the first set of evidence (against a feature-tuned remapped response) from a sensory area with neurons that are more finely tuned to stimulus features. The weak effect found in our data may either reflect a feature-selective input to the remapped response or simply the effects of response adaptation given the slightly higher response in the presaccadic period when the monkey was attending to the preferred direction outside the RF. These presaccadic effects could themselves reflect weak stimulus-driven effects from outside the RF [17] and/or the effects of feature-based attention [18].

MT neurons do not show anticipatory remapping [13]; we hypothesize that the anticipatory remapping seen in attentional and oculomotor control areas like LIP, FEF, and SC is part of the process that switches the attentional pointer, and though this process starts before the saccade in these areas, its effects in MT only manifest after the saccade (at a point of time when the pointer is again at the task-relevant location). The anticipatory nature of the remapping seen in LIP, FEF, and SC may confer an evolutionary advantage by ensuring that attention is allocated to the correct retinotopic location soon after the saccade. A recent psychophysical study [28], using a motion task similar to ours, observed a decrement in performance at attended locations before a saccade and suggested that this resulted from the known reallocation of attention to the saccade target [34,48–50] and/or the remapped location [27]. Our data from MT do not indicate any evidence for a presaccadic shift of attention to the remapped location. Recordings from areas upstream of MT along the motion-process pathway combined with psychophysical measurements of perisaccadic attentional dynamics are needed before the neural basis of these

processes can be understood. Our current results, when combined, resolve important issues concerning the perisaccadic representation of visual stimuli in the dorsal stream and demonstrate a significant role for top-down attention in modulating this representation.

Materials and Methods

Statement on Animal Research within This Study

All animal work was conducted according to the relevant national and international guidelines. All animal procedures have been approved by the responsible regional government office (Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit [LAVES]) under the permit numbers 33.14.42502-04-064/07 and 3392 42502-04-13/1100.

The animals were group-housed with other macaque monkeys in facilities of the German Primate Center in Goettingen, Germany in accordance with all applicable German and European regulations. The facility provides the animals with an enriched environment (including a multitude of toys and wooden structures) exceeding the size requirements of the relevant European regulations.

All invasive procedures were done under appropriate anesthesia and with appropriate analgesics. The German Primate Center has several veterinarians on staff that regularly monitor and examine the animals and consult on any procedures.

During the study, the animals had unrestricted access to food and fluid, except on the days when data were collected or the animal was trained on the behavioral paradigm. On these days, the animals were allowed unlimited access to fluid through their performance in the behavioral paradigm. Here, the animals received fluid rewards for every correctly performed trial. Throughout the study, the animals' psychological and veterinary wellbeing was monitored by the veterinarians, the animal facility staff, and the lab's scientists, all specialized on working with nonhuman primates.

Both of the animals used in the study are currently in other studies in our laboratory.

General

We trained two male rhesus monkeys (*Macaca mulatta*), monkey H and monkey E, to perform a demanding visuospatial-attention task along with a saccade. Each monkey was implanted with a titanium head holder and a recording chamber located above the parietal cortex (based on a MRI scan) to allow MT recordings. All surgical procedures were approved by the district government of Lower Saxony, Germany, and were conducted under general anesthesia using standard techniques. The experiments were performed in a dimly lit room, and the monkey viewed a CRT monitor (76 Hz) while sitting in a custom-made primate chair during the experiment (see S1 Text for detailed Methods). All aspects of the experiment were controlled by custom software running on an Apple Macintosh computer. The eye position was monitored by an EyeLink 1000 (SR Research, Canada) system at 1,000 Hz. Neuronal activity was recorded extracellularly with a 5-channel micro drive system (Mini Matrix, Thomas Recording, Giessen, Germany) and processed using the Plexon data acquisition system (Plexon Inc., Dallas, TX, United States). Only data from well-isolated neurons are reported here. MT was identified by referencing the recordings to the structural MRI and by the physiological properties of the recorded neurons.

Behavioral Tasks and Stimuli

Once a neuron was isolated, we mapped its RF location and determined the neurons' preferred direction and speed while the monkeys performed a fixation task. We then switched to the main experiment (Fig 1), in which each trial was composed of one of four tasks (three

experimental tasks and one control task, chosen in a pseudo-randomly interleaved manner). In all four tasks, the monkeys initiated the trial by holding a metal bar and foveating a black fixation point. In the control task (the "simple-saccade" task, 11.1% of trials), the monkeys had to maintain fixation until a saccade target (identical to the fixation point) appeared and the fixation point disappeared (see S1 Text for details). The monkeys had to make a saccade to the saccade target and maintain fixation there until the end of the trial to obtain a reward. In the three experimental tasks, in addition to potentially making a saccade as in the simple-saccade task, the monkeys had to attend to one of two moving RDPs (both moving in the same direction, which was either the neuron's preferred or antipreferred direction) and respond to a brief (132 ms) direction change in this target by releasing the bar, but ignore similar changes in the other RDP (the distractor). The target stimulus was cued by a stationary RDP that appeared at its location for 263 ms. The target and distractor stimuli were always equidistant from the fixation point and saccade target and were always mirrored with respect to the saccade target (Fig 1), so that for horizontal saccades, they appeared in the upper and lower hemifield (and the left or right hemifield, if the RF was located in the left [monkey H] hemifield or right [monkey E], respectively). The cue appeared equally often in the postsaccadic RF (attend-in condition) or opposite to it (attend-out condition). In addition, during the trial, if the fixation point jumped to a new location (as in the simple-saccade task), the monkeys had to refixate the fixation point while continuing to attend to the cued target. In the first of the three experimental tasks (the "continuous-stimulus task," 22.2% of trials), the fixation point jumped to its new location 671 ms after RDP onset. The direction change in the target RDP could occur between 974 and 1,895 ms after the fixation point jumped. The second experimental task (the "interrupted-stimulus task," 44.4% of trials) was similar to the continuous-stimulus task, but the target and distractor RDPs disappeared 105 ms after the fixation point jumped and, therefore, no stimulus ever appeared in the neurons' RF after the saccade (or before the saccade). The monkeys had to simply make a saccade to the new fixation point location and maintain fixation until the end of the trial to obtain a reward; the few trials with saccades that started before the disappearance of the stimulus were discarded. The third experimental task (the "fixation task," 22.2% of trials) was also similar to the continuous-stimulus task except that the fixation point never jumped, and the direction change in the target RDP occurred 789 to 1,842 ms after RDP onset. This task was included to make sure the monkeys paid attention to the target even during the time when they made a saccade in the other two experimental tasks, and was not analyzed further for this study. Distractor changes occurred on about 37.5% of trials (in the continuous-stimulus and fixation tasks) and never more than once on each trial. The timing of distractor changes overlapped that of target changes, with the additional requirement that any distractor change occurred at least 500 ms before the target change on each trial. This separation ensured that the monkeys' rare responses to the distractor change could be easily identified and distinguished from their responses to the target change. In all the tasks, the background was always grey, and the fixation point and RDPs, including the stationary cue, were black. Our use of black stimuli addresses concerns regarding the persistence of white visual stimuli on black backgrounds after their stipulated disappearance from a CRT monitor.

Data Analysis

We detected saccades using a velocity threshold criterion that was validated by visual inspection. We included data from all neurons that showed a significantly greater postsaccadic response to at least one of the two directions in the continuous-stimulus task (compared to the simple saccade task in which there is no stimulus in the RF, i.e., they were visually responsive to the RDP) as well as a significant difference between the responses to the two RDP directions in the continuous-stimulus task (i.e., they showed direction tuning). Additionally, we excluded

neurons in which the onset of the RDP at the (future) postsaccadic RF location elicited a statistically significant response from the neuron. Only correctly completed trials were analyzed. PSTHs (Figs 2–4) were calculated using partially overlapping bins (50 ms width, stepped every 10 ms). For the interrupted-stimulus task (Figs 3–5), we used a time window from 0 to 350 ms after saccade offset, as a compromise duration that was long enough to make statistically meaningful statements about the effects we observed, and yet not so long that the monkeys would have ample time to withdraw attention from the attended spatial location after realizing that the attended stimulus had disappeared. In addition, 350 ms is roughly equal to a typical intersaccadic interval. For the continuous-stimulus task (Fig 2), our goal was to merely confirm that we found the attentional effects expected from MT in our dataset. For a precise estimate, we chose a time window of 0 to 500 ms. This choice is not critical, and using a time window of 0 to 350 ms would not affect our conclusions (though it would provide a less precise estimate). The modulation index was defined as the difference in the firing rates for the two conditions divided by their sum. A direction-tuning index was similarly defined as the difference in firing rates for preferred and antipreferred directions divided by their sum (Fig 5). We report medians and use *p*-values from Wilcoxon signed-rank tests throughout.

Supporting Information

S1 Fig. The memory trace does not start earlier than the sensory response. The memory trace, plotted as the difference between the response in the attend-in condition of the interrupted-stimulus task and the response in the simple-stimulus task (mean difference across neurons and SEM—red trace), arises at the same time or later than the sensory response, plotted as the difference between the response in the continuous-stimulus task with the preferred direction and the response in the simple-stimulus task (mean difference across neurons and SEM—blue trace). The contribution of predictive remapping to the timing of the steep rise of the sensory response toward its peak would be minimal, and the memory trace does not appear to lead the sensory response anywhere along this steep rise. In order to facilitate comparison, both traces were normalized by subtracting the mean value of the trace from -300 to 0 ms and then dividing by the maximum value. Data for monkey H (A) and monkey E (B). Other conventions as in Fig 2. Data in Supporting Information (S6 Data).
(PDF)

S2 Fig. Attentional effects in the continuous task manifest at or after saccade offset. The attentional effect in the continuous-stimulus task for the preferred direction, plotted as the difference between the responses in the attend-in (Fig 2, blue curve) and attend-out (Fig 2, red curve) conditions (mean and 95% confidence bands), rises above zero only after saccade offset. Data for monkey H (A) and monkey E (B). Other conventions as in Fig 2. Data in Supporting Information (S7 Data).
(PDF)

S1 Data. The data presented in Fig 2 are tabulated in separate text files contained in the zipped folder.
(ZIP)

S2 Data. The data presented in Fig 3 are tabulated in separate text files contained in the zipped folder.
(ZIP)

S3 Data. The data presented in Fig 4 are tabulated in separate text files contained in the zipped folder.
(ZIP)

S4 Data. The data presented in Fig 5 (and in the associated portion of the Results section) are tabulated in separate text files contained in the zipped folder.
(ZIP)

S5 Data. The data presented in Fig 6 are tabulated in separate text files contained in the zipped folder.
(ZIP)

S6 Data. The data presented in S1 Fig are tabulated in separate text files contained in the zipped folder.
(ZIP)

S7 Data. The data presented in S2 Fig are tabulated in separate text files contained in the zipped folder.
(ZIP)

S1 Text. Detailed Materials and Methods.
(PDF)

Author Contributions

Conceived and designed the experiments: TY BSK. Performed the experiments: TY BSK. Analyzed the data: TY BSK. Contributed reagents/materials/analysis tools: TY ST BSK. Wrote the paper: TY ST BSK.

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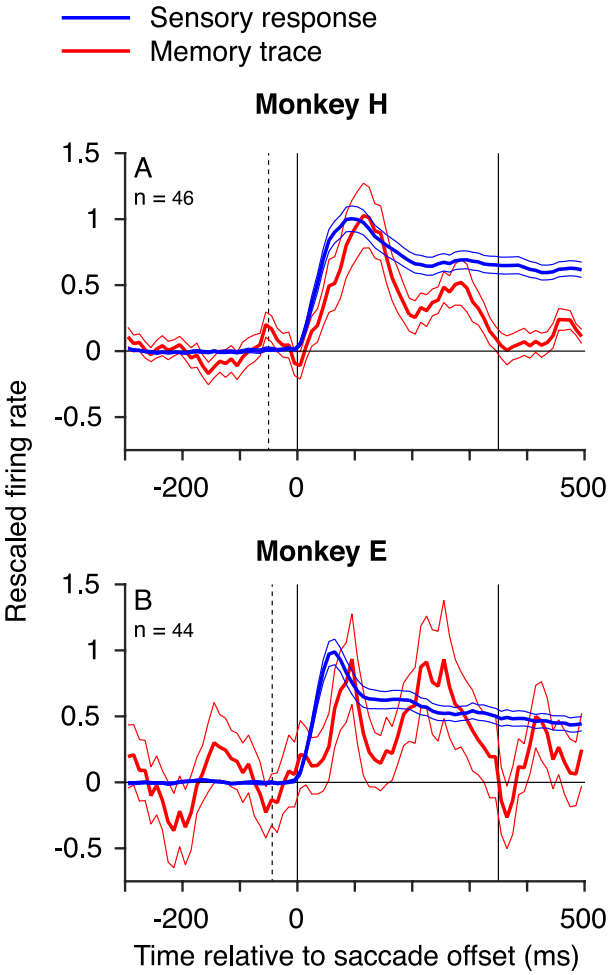

Figure S1: The memory trace does not start earlier than the sensory response. The memory trace, plotted as the difference between the response in the attend-in condition of the interrupted stimulus task and the response in the simple-stimulus task (mean difference across neurons and SEM – red trace), arises at the same time or later than the sensory response, plotted as the difference between the response in the continuous stimulus task with the preferred direction and the response in the simple-stimulus task (mean difference across neurons and SEM – blue trace). The contribution of predictive remapping to the timing of the steep rise of the sensory response towards its peak would be minimal, and the memory trace does not appear to lead the sensory response anywhere along this steep rise. In order to facilitate comparison, both traces were normalized by subtracting the mean value of the trace from -300 to 0 ms, and then dividing by the maximum value. Data for monkey H (A) and monkey E (B). Other conventions as in Fig 2. Data in Supporting Information (S6 Data).

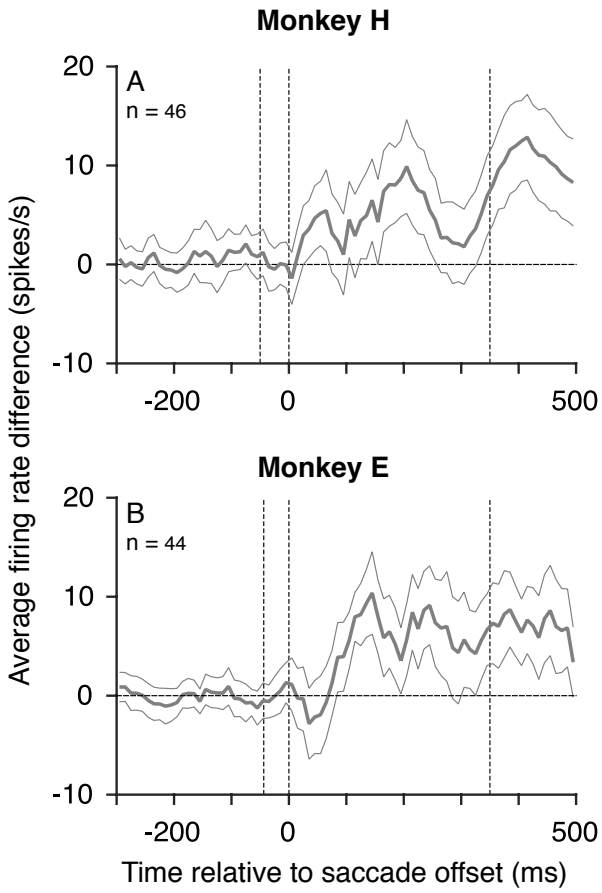

Figure S2: Attentional effects in the continuous task manifest at or after saccade offset. The attentional effect in the continuous task for the preferred direction, plotted as the difference between the responses in the attend-in (Fig 2, blue curve) and attend-out (Fig 2, red curve) conditions (mean and 95 % confidence bands), rises above zero only after saccade offset. Data for monkey H (A) and monkey E (B). Other conventions as in Fig 2. Data in Supporting Information (S7 Data).

Supporting information

Methods

This is an expanded version of the Methods section in the main text. We trained two male rhesus monkeys (Macaca mulatta, 7–11 kg), monkey H and monkey E, to perform a demanding visuospatial-attention task along with a saccade. Each monkey was implanted with a titanium head holder to minimize head movements during the experiment. One recording chamber was also implanted in each monkey above the left (monkey E) or the right (monkey H) parietal cortex to allow access to MT, with implantation locations chosen based on a preceding MRI scan. All procedures were approved by the district government of Lower Saxony, Germany, and all surgeries were conducted under general anesthesia using standard techniques.

The experiments were performed in a dimly-lit room with the only source of light being the display monitor. A CRT monitor (Sony Trinitron GDM-FW900) at a distance of 57 cm from the monkey was used to display the visual stimulus at a refresh rate of 76 Hz and a spatial resolution of 40 pixels/degree. The monkey sat in a custom-made primate chair during the experiment. Stimulus presentation, reward delivery, electrophysiological and behavioral data collection was controlled by custom software and run on an Apple Macintosh computer. All stimulus onsets and durations were specified in terms of number of frames (CRT monitor refreshes), and the times reported here in millisecond units are correct to within 13 ms (the duration of one frame), given the vertical scan-rate properties of the CRT monitor. The animals received a fluid reward immediately following each correct trial. The eye-position was monitored by an EyeLink 1000 (SR Research, Canada) system at 1000 Hz. Neuronal activity was recorded extracellularly with a 5-channel micro drive system (Mini Matrix, Thomas Recording, Giessen, Germany) and processed using the Plexon data acquisition system (Plexon Inc., Dallas, TX). Only data from well-isolated neurons were used for the analysis. MT was identified by referencing the recordings to the structural MRI and by the physiological properties of the recorded neurons: most

neurons were direction-tuned, the average diameter of the receptive fields (RFs) was approximately equal to the RF eccentricity and there was a predictable progression of RF centers at different locations along the superior temporal sulcus.

Behavioral tasks and stimuli

Once a neuron was isolated and while the monkey performed a fixation task, we located the RF by moving a stationary circular random dot pattern (RDP) across the screen using a mouse. During this task, the monkey had to maintain fixation on a fixation point and respond to a brief luminance change at the fixation point. We then determined the neuron's preferred direction and speed, again while the monkey performed a fixation task (usually at the location of the saccade target in the main task), by presenting a RDP with moving dots within a circular aperture in the RF, changing the direction and speed every 250 ms picked from a set of 3 possible speeds (4, 8 or 16 degrees per second) and 12 possible directions (evenly separated by 30 degrees around a circle). The preferred and anti-preferred directions, and the preferred speed were used in the main experiment. Occasionally, we recorded simultaneously from two or more neurons with overlapping RFs when their preferred directions also overlapped or were opposite to each other.

After identifying the RF location and preferred direction, we switched to the main experiment. In the main experiment (Figure 1), each trial was composed of one of four tasks (three experimental tasks and one control task, chosen in a pseudo-randomly interleaved manner). For all four tasks, the monkeys initiated the trial by holding a lever and foveating a black fixation point. In the control task (the "simple-saccade" task), performed on 11.1 % of trials, a saccade target, identical to the fixation point, appeared between 10 and 20 degrees eccentrically (value fixed for each neuron, and either 15 or 20 degrees in most cases),1382 ms after the monkey initiated fixation. The saccade target then stayed on for 1368 ms (the end of the trial). Saccades were always either horizontal or vertical. In all tasks, there was a

one-frame (13 ms) overlap between the fixation point and the saccade target, so that the fixation point disappeared one frame after the saccade target appeared: perceptually, the fixation point appeared to jump from its original location to the saccade target. Once the fixation point jumped, the monkey had to make a saccade to the new location of the fixation point within 263 ms and maintain fixation until the end of the trial in order to obtain a reward for correct performance. In the three experimental tasks, after 118 ms of fixation, a stationary RDP cue within a circular aperture (of the same size as the target), which indicated the location of the future target of attention, was presented for 263 ms either in the neurons' post-saccadic RF (attend-in condition) or opposite to it (attend-out condition) equally often. After an additional delay of 329 ms following cue offset, two moving RDPs (2 degrees in radius, all dots moving in the same direction of motion and within stationary circular apertures) were presented on the screen, with both moving equally often in the neurons' preferred or anti-preferred direction. One of them, the target was located at the previously cued location, while the other, the distractor, was located opposite to it (i.e. reflected across the horizontal or vertical meridian, see Figure 1). The monkeys' task was to respond to a brief (132 ms) direction change in the target by releasing the lever (within 600 ms of the change), but ignore similar changes in the distractor. In addition, during the trial, if the fixation point jumped to a new location (as in the "simple-saccade" task), the monkeys had to refixate the fixation point while continuing to attend to the cued target. In the first of the three experimental tasks (the "continuous-stimulus task", 22.2 % of trials), the fixation point jumped to its new location 671 ms after RDP onset. The direction change in the target RDP could occur between 974 ms to 1895 ms after the fixation point jumped. The second experimental task (the "interrupted-stimulus task", 44.4 % of trials) was similar to the continuous-stimulus task, and the fixation point jumped at the same time as in the continuous-stimulus task, but the target and distractor RDPs disappeared 105 ms after the fixation point jumped. Therefore, on these trials, no stimulus ever appeared in the neurons' RF after the saccade (or before the saccade). The monkeys had to simply make a saccade to the new fixation point location and maintain fixation until the end of the trial to obtain a reward. The

few trials with saccades that started before the disappearance of the stimulus were discarded. The third experimental task (the “fixation task”, 22.2 % of trials) was also similar to the continuous-stimulus task, except that the fixation point never jumped, and the direction-change in the target RDP occurred 789 ms to 1842 ms after RDP onset. This task was included to make sure the monkeys paid attention to the target even during the time when they made a saccade in the other two experimental tasks, and was not analyzed further for this study.

In all the tasks, the background was always grey with a luminance of 14.2 cd/m^2, and the fixation point and RDPs including the stationary cue were black with the luminance of 0.68 cd/m^2. Our use of black stimuli minimizes the concerns that arise when white stimuli are used on a black background regarding the persistence of visual stimuli on the display monitor after their stipulated disappearance. Individual RDP dot size was 0.1° x 0.1°, and the dot density was 10 dots/deg^2. Monkeys had to maintain fixation within a circular window of 2 degrees radius around the fixation point, except for a period of 263 ms after the fixation point jumped to give them time to make the saccade. The saccade direction was set according to the position of the RF: for example, if the RF center was directly above or below the fixation point, we used a horizontal saccade, while if the RF center was directly to the left or right of the fixation point, we used a vertical saccade. If the RF center was offset both vertically and horizontally from the fixation point, the choice was no longer critical, but we usually used a horizontal saccade.

Data analysis

We only included correctly performed trials in our analysis. After excluding fixation breaks, both monkeys performed the tasks correctly on over 94.6 % of trials. Data analysis was performed using custom software in MATLAB (MATLAB Inc, Natick, MA). We included data from all neurons that showed a

significantly greater post-saccadic response to at least one of the two directions in the continuous-stimulus task (compared to the simple saccade task where there is no stimulus in the RF, i.e. they were visually responsive to the RDP) as well as a significant difference between the responses to the two RDP directions in the continuous-stimulus task (i.e. they showed direction tuning). Additionally, we excluded neurons where the onset of the RDP at the (future) post-saccadic RF location elicited a statistically significant response from the neuron. Peri-stimulus time histograms (PSTHs: Figures 2-4) were calculated using partially overlapping bins (50 ms width, stepped every 10 ms): the mean activity for each neuron across trials was first calculated and then these mean PSTHs for individual neurons were averaged across neurons to obtain the displayed PSTHs. For the differences between conditions (say A and B), we report the effects using a modulation index, which is defined in the usual manner for each neuron as the difference in the firing-rates for the two conditions divided by their sum. A direction-tuning index was similarly defined as the difference in firing-rates for preferred and anti-preferred directions divided by their sum (Figure 5). We report the average modulation and direction-tuning indices using the median value after converting it back into a percentage. For the analyses of the memory trace in Figures 3 and 4, because we did not find a difference between the response in the interrupted-stimulus task based on whether the RDP was moving in the preferred or anti-preferred direction before the saccade (Figure 5), we pooled the trials irrespective of RDP direction and only separated the trials into those where the monkey was cued to attend to the post-saccadic RF location (attend-in condition) and those where the monkey was cued to attend outside it (attend-out condition).

We detected saccades using a standard velocity-threshold algorithm: onset (and offset) times were determined by when the eye velocity exceeded (and then dropped below) 30 degrees per second. This threshold value was set to lie clearly above the peak excursions of the baseline noise in the eye-velocity traces, and the algorithm was validated by visual inspection for each monkey. In addition to the large saccade from the fixation point to the saccade target (to which we aligned our data for our analyses), both

monkeys also made small-amplitude eye-movements within the fixation window while fixating: these eye-movements could be observed to induce a short-duration transient response lasting less than 100 ms when there was a motion stimulus in the RF [as has been reported earlier: 1]. For the main analyses of interest in this paper, there was no stimulus in the RF after the saccade and no transient response was detected following the microsaccade. Even so, we re-examined our results and conclusions after discarding spikes elicited within 100 ms after any small eye movement occurring after the large refixation saccade, within the time-windows of interest. This correction was made both for the PSTHs and for the statistical comparisons based on spike-counts. We verified that our results remain similar and that our conclusions remain robust when such a correction for small eye-movements is made.

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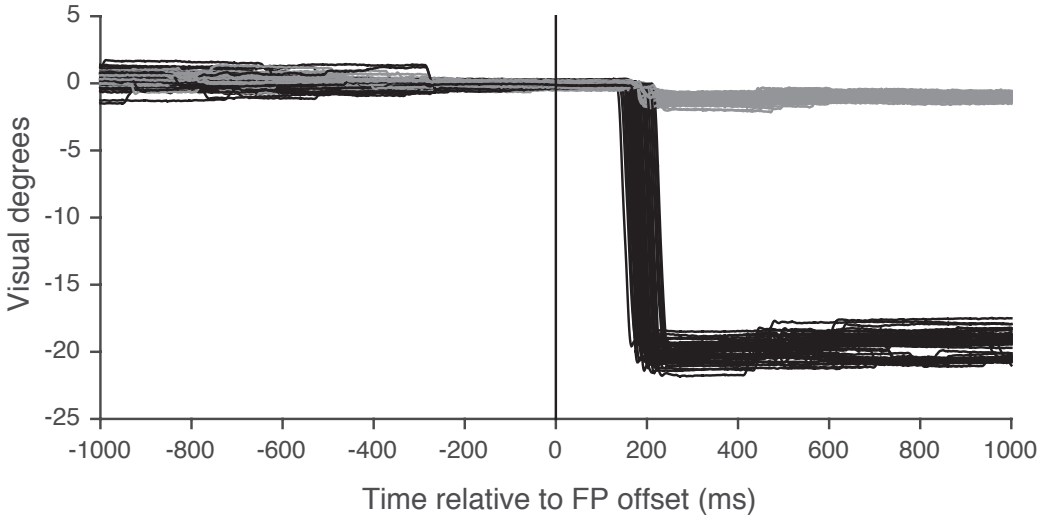
Additional supplementary materials 1: Example eye traces



The example eye traces of trial No. 80-180 from Monkey E in the experiment when he was performing the task and made a sacccade in that trial. The black and gray traces indicate the horizontal and vertical eye position respectively. In this session, the animal was required to perform a 20 visual angle degrees saccade to the left when he saw the fixation point jump. (recording session: tao-trAttC-edg-047-001+02).

Additional supplementary materials 2: Cells list

Note:
Depth: the zero point of the depth was the tip of the guide tube (ideally, it should be right under the dura).
Signal: If the number isbetween 8 - 10, it was a well-isolated unit.
Sac ampl (visual degree): saccade amplitude, the required saccade amplitude the animals should made in a given experiment.
xCo and yCo (mm): the x y coordinates of the recording site.
RFx, RFy (visual degree): the x and y coordinates of the receptive field. Minus means left in x and up in y.
PreS in cell (visual degree per second): the preferred speed of the neuron.
PreS in exp (visual degree per second): the speed of the stimuli in the experiment
PD in cell (visual degree): the preferred motion direction of the neuron.
The blank cells mean the data was unavailable, or could be found in the data.

date	*filename*	*channel*	*eletrode #*	*xCo*	*yCo*	*depth*	*linear tunning*	*signal*	*spiral tuning*	*Sac ampl*	*StiSize*	*SacDir*	*RFx*	*RFy*	*RFsize*	*PreS in cell*	*PreS in exp*	*PD in exp (degree)*	*PD in cell (degree)*
130919	tao-trAttC-edg-008-001+01	5b	5	-2,4	-4	13798		8	0	20	80	left	5,5	-11	0		16	150	
130919	tao-trAttC-edg-008-001+01	3a	3	-2,4	-4	13482		8	0	20	80	left	5,5	-11	0	16	16	150	150-180
130919	tao-trAttC-edg-008-001+01	3b	3	-2,4	-4	13482		8	0	20	80	left	5,5	-11	0		16	150	
130923	tao-trAttC-edg-010-001+01	5a	5	-2	-4	13629		9	0	20	80	left	7	-11	0	8	4	150	120-180
130923	tao-trAttC-edg-010-001+01	5b	5	-2	-4	13629		8	0	20	80	left	7	-11	0		4	150	
130923	tao-trAttC-edg-010-001+01	3b	3	-2	-4	13307		8	0	20	80	left	7	-11	0	16	4	150	300-330
130926	tao-trAttC-edg-013-001+01	2a	2	-2	-6,8	13206		8	0	20	80	left	8	8,5	0		16	60	
130926	tao-trAttC-edg-013-001+01	2b	2	-2	-6,8	13206		8	0	20	80	left	8	8,5	0		16	60	
130926	tao-trAttC-edg-013-001+01	1a	1	-2	-6,8	12726		8	0	20	80	left	8	8,5	0		16	60	
130926	tao-trAttC-edg-013-001+01	4a	4	-2	-6,8	12676		8	0	20	80	left	8	8,5	0		16	60	
130926	tao-trAttC-edg-013-001+01	4b	4	-2	-6,8	12676		8	0	20	80	left	8	8,5	0		16	60	
130926	tao-trAttC-edg-013-001+01	3a	3	-2	-6,8	11582		8	0	20	80	left	8	8,5	0	8--16	16	60	30-90
130926	tao-trAttC-edg-013-001+01	3b	3	-2	-6,8	11582		8	0	20	80	left	8	8,5	0	8--16	16	60	30-60
130926	tao-trAttC-edg-013-001+01	5a	5	-2	-6,8	11398		8	0	20	80	left	8	8,5	0	8--16	16	60	30-60
130926	tao-trAttC-edg-013-001+01	5b	5	-2	-6,8	11398		8	0	20	80	left	8	8,5	0	8--16	16	60	30-60
130926	tao-trAttC-edg-013-001+01	5b	5	-2	-6,8	11347		8	0	20	80	left	8	8,5	0		16	60	
131001	tao-trAttC-edg-016-001+01	3a	3	-1,8	-7	13034		8	0	20	80	left	10	13	0	16	16	90	30-120
131001	tao-trAttC-edg-016-001+01	3b	3	-1,8	-7	13034		8	0	20	80	left	10	13	0	16	16	90	30-120
131003	tao-trAttC-edg-018-001+01	2b	4	-2,5	-5,5	16252		8	0	20	80	up	10	2	0	16	16	300	300
131003	tao-trAttC-edg-018-001+01	4a	4	-2,5	-5,5	16252		8	0	20	80	up	10	2	0	4	16	300	60
131003	tao-trAttC-edg-018-001+01	2a	2	-2,5	-5,5	15898		8	0	20	80	up	10	2	0	16	16	300	300-0
131004	tao-trAttC-edg-019-001+01	1a	1	-1,8	-7	13337		8	0	20	80	left	6	11	0		8	120	

131004	tao-trAttC-edg-019-001+01	2a	2	-1,8	-7	13083	8	0	20	80	left	6	11	0	8	8	120	90-120
131004	tao-trAttC-edg-019-001+01	2b	2	-1,8	-7	13083	8	0	20	80	left	6	11	0	8	8	120	120-150
131008	tao-trAttC-edg-021-001+01	4a	4	-3	-4	16229	8	0	20	80	left	5,5	9	0		8	180	
131008	tao-trAttC-edg-021-001+01	4b	4	-3	-4	16229	8	0	20	80	left	5,5	9	0		8	180	
131008	tao-trAttC-edg-021-001+01	3a	3	-3	-4	15598	8	0	20	80	left	5,5	9	0		8	180	
131008	tao-trAttC-edg-021-001+01	5a	5	-3	-4	15420	8	0	20	80	left	5,5	9	0	8	8	180	180-210
131009	tao-trAttC-edg-022-001+01	4a	4	-4	-4	16252	8	0	20	80	left	4	-7,5	0		16	0	
131009	tao-trAttC-edg-022-001+01	2b	2	-4	-4	15776	8	0	20	80	left	4	-7,5	0		16	0	
131009	tao-trAttC-edg-022-001+01	2a	2	-4	-4	15776	8	0	20	80	left	4	-7,5	0		16	0	
131011	tao-trAttC-edg-024-001+01	3a	3	-3,5	-4	15637	8	0	15	80	down	9	-3	0	16	16	90	90
131011	tao-trAttC-edg-024-001+01	3b	3	-3,5	-4	15637	8	0	15	80	down	9	-3	0	16	16	90	90
131011	tao-trAttC-edg-024-001+01	4a	4	-3,5	-4	14043	8	0	15	80	down	9	-3	0	16	16	90	90
131011	tao-trAttC-edg-024-001+01	2a	2	-3,5	-4	13939	8	0	15	80	down	9	-3	0	16	16	90	90
131014	tao-trAttC-edg-025-001+01	3a	3	-3	-3,5	15637	8	0	20	80	left	2,5	-11	-1	8--16	16	210	180-239
131014	tao-trAttC-edg-025-001+01	3b	3	-3	-3,5	15637	8	0	20	80	left	2,5	-11	0	8--16	16	210	180-240
131014	tao-trAttC-edg-025-001+01	1a	1	-3	-3,5	15397	8	0	20	80	left	2,5	-11	0	16	16	210	210
131014	tao-trAttC-edg-025-001+01	2a	2	-3	-3,5	14746	8	0	20	80	left	2,5	-11	0		16	210	
131015	tao-trAttC-edg-026-001+01	2a	2	-4	-5	13520	8	0	10	80	up	5	0	0	4	4	60	60
131016	tao-trAttC-edg-027-001+01	1a	1	-3	-3	14700	8	0	15	80	up	6,5	1	0	16	16	90	30-90
131016	tao-trAttC-edg-027-001+01	5a	5	-3	-3	14572	8	0	15	80	up	6,5	1	0		16	90	
131016	tao-trAttC-edg-027-001+01	5b	5	-3	-3	14572	8	0	15	80	up	6,5	1	0		16	90	
131126	tao-trAttC-edg-030-001+01	4a	4	-1	-7	9780	9	0	15	80	right	4	9	0	16	16	270	240-270
131126	tao-trAttC-edg-030-001+01	4b	4	-1	-7	9780	9	0	15	80	right	4	9	0	16	16	270	210-270
131126	tao-trAttC-edg-030-001+01	1a	1	-1	-7	9442	8	0	15	80	right	4	9	0	4	16	270	240
140220	tao-trAttC-edg-038-001+01	1a	1	-0,8	-6,8	8967	8	0	20	80	left	10	11	0	16	16	300	300-330
140225	tao-trAttC-edg-040-001+01	5b	5	-0,5	-6,6	8643	8	0	15	80	left	7	12	0		16	240	
140227	tao-trAttC-edg-042-001+01	5b	5	-1	-6	9860	8	0	15	80	left			0		16	90	
140227	tao-trAttC-edg-042-001+02	5a	5	-1	-6	9956	8	0	15	80	left			0		16	90	
140304	tao-trAttC-edg-044-001+01	5a	5	-0,7	-6,7	8220	9	0	15	80	left	7	11	0	16	16	330	330
140304	tao-trAttC-edg-044-001+02	5a	5	-0,7	-6,7	8165	8	0					excluded , not sure if in MT					
140304	tao-trAttC-edg-044-001+02	3a	3	-0,7	-6,7	8125	8	0	15	80	left	7	11	0	16	16	210	210
140305	tao-trAttC-edg-045-001+01	5a	5	-0,7	-6,7	9420		0					excluded , not sure if in MT					
140305	tao-trAttC-edg-045-001+02	3a	3	-0,7	-6,7	9660		0					excluded , not sure if in MT					
140307	tao-trAttC-edg-046-001+01	5b	5	-0,5	-7,2	8130		0					excluded , not sure if in MT					
140307	tao-trAttC-edg-046-001+01	3a	3	-0,5	-7,2	8040		0					excluded , not sure if in MT					
140307	tao-trAttC-edg-046-001+01	4a	4	-0,5	-7,2	7764		0					excluded , not sure if in MT					
140307	tao-trAttC-edg-046-001+02	5a	5	-0,5	-7,2	8130		0					excluded , not sure if in MT					
140311	tao-trAttC-edg-047-001+01	5a	5	-0,8	-7	8527		0					excluded , not sure if in MT					
140311	tao-trAttC-edg-047-001+02	5a	5	-0,8	-7	8527	8	0	20	80	left	12	12	0	16	16	90	90
140318	tao-trAttC-edg-051-001+01	5b	5	-1,1	-7,2	10898	8	0	20	80	left	12	12	0	16	16	90	90

140318	tao-trAttC-edg-051-001+01	5a	5	-1,1	-7,2	10898	9	0	15	80	up	12	0,5	0	16	16	330	330
140318	tao-trAttC-edg-051-001+02	5a	5	-1,1	-7,2	11232	8	0	15	80	up	10	1	0	4	4	270	270
140318	tao-trAttC-edg-051-001+02	5b	5	-1,1	-7,2	11232	8	0	15	80	up	10	1	0	4	4	270	270
140318	tao-trAttC-edg-051-001+02	4a	4	-1,1	-7,2	10306	8	0	15	80	up	10	1	0		4	270	
140610	tao-trAttC-edg-073-001+01	4a	4	-2	-5	9920	8	0	15	80	up	10	1	0	16	16	30	30
140610	tao-trAttC-edg-073-001+02	4b	4	-2	-5	9836	7--8	0	15	80	up	10	1	0	16	16	30	30
140611	tao-trAttC-edg-074-001+01	4a	4	-1,2	-7,2	8517	8	0	20	80	left	10	1	0	16	16	180	180
140612	tao-trAttC-edg-075-001+02	4a	4	-1,4	-7	7600	8	0	20	80	left	10	11	0	16	16	270	270-300
140613	tao-trAttC-edg-076-001+01	5a	5	-1,5	-7,3	8913	8	0	20	80	left	11	11	0	16	16	60	60
140613	tao-trAttC-edg-076-001+01	4b	4	-1,5	-7,3	8114	8	0	20	80	left	11	11	0	16	16	60	60
140613	tao-trAttC-edg-076-001+02	4a	4	-1,5	-7,3	8500		0					excluded, not enough trials					
140617	tao-trAttC-edg-077-001+01	5a	5	-1	-6,7	9451	8	0	15	80	left	5	11	0	4--16	4	180	150-180
140617	tao-trAttC-edg-077-001+02	5a	5	-1	-6,7	9220		0					excluded, not enough trials					
140617	tao-trAttC-edg-077-001+02	5b	5	-1	-6,7	9220		0					excluded, not enough trials					
140618	tao-trAttC-edg-078-001+01	5a	5	-1,3	-6,6	10728	8	0	15	80	up	11	2,5	0	16	16	300	300
140618	tao-trAttC-edg-078-001+02	4a	4	-1,3	-6,6	11110	8	0	12,5	80	up	10	0	0	16	16	60	60
140618	tao-trAttC-edg-078-001+02	4b	4	-1,3	-6,6	11110	8	0	12,5	80	up	10	0	0	4	16	60	120
140619	tao-trAttC-edg-079-001+01	5a	5	-1,4	-7	10098	8	0	15	80	left	4	6	0	16	16	330	330
140619	tao-trAttC-edg-079-001+01	5b	5	-1,4	-7	10098	8	0	15	80	left	4	6	0	16	16	330	
140619	tao-trAttC-edg-079-001+02	5a	5	-1,4	-7	9835	8	0	15				excluded, not enough trials					
140619	tao-trAttC-edg-079-001+02	5b	5	-1,4	-7	9835	8	0	15				excluded, not enough trials					
140619	tao-trAttC-edg-079-001+03	5a	5	-1,4	-7	9835	8	0	15	80	left	5	6	0		16	330	
140619	tao-trAttC-edg-079-001+03	5b	5	-1,4	-7	9835	8	0	15	80	left	5	6	0		16	330	
140624	tao-trAttC-edg-080-001+02	5a	5	-1	-7	8151	8	0	15	80			excluded , not sure if in MT					
140625	tao-trAttC-edg-081-001+01	5a	5	-2	-6,8	10207	8	0	15	80	left	3	7	0	16	16	30	30
140625	tao-trAttC-edg-081-001+02	3a	3	-2	-6,8	10321		0	15	80			excluded, not enough trials					
140625	tao-trAttC-edg-081-001+02	3b	3	-2	-6,8	10321		0	15	80			excluded, not enough trials					
140625	tao-trAttC-edg-081-001+03	3a	3	-2	-6,8	10211	8	0	15	80	up	11	0,5	0	16	16	0	0
140626	tao-trAttC-edg-082-001+01	3a	3	-2	-7	10590	8	0	15	80	up	11	1	0	16	16	180	150-180
140626	tao-trAttC-edg-082-001+02	3a	3	-2	-7	10321	8	0	15	80	up	10	1	0	16	16	180	180
140626	tao-trAttC-edg-082-001+03	2a	3	-2	-7	10211	8	0	15	80	up	10	3	0	4	16	180	0
140627	tao-trAttC-edg-083-001+01	5a	5	-2	-7	11040	8	0	15				excluded, not enough trials					
140701	tao-trAttC-edg-084-001+01	3a	3	-2	-7	8830	8	0	15	80	left	3	8	0	16	16	0	0
140701	tao-trAttC-edg-084-001+03	3a	3	-2	-7	8720	8	0	15	80	left	3	8	0	16	16	0	0
140701	tao-trAttC-edg-084-001+03	3b	3	-2	-7	8720	8	0	15	80	left	3	8	0	16	16	0	0

120209	tao-trAttC-hay-381-001+01	5a	4	-1,3	-1,3	8004	9	0	20		right	-16	-8	0		8	180	150-210
120209	tao-trAttC-hay-381-001+02	3a	3	-1,3	-1,3	8669	8	0	20		up	-16	-8	0		8	180	180-240

120209	tao-trAttC-hay-381-001+02	5b	5	-1,3	-1,3	8652	8	0	20	up	-16	-8	0		8	180	180
120210	tao-trAttC-hay-382-001+02	3a	3	-1,3	-1,5	9161	9	0	20	up	-15,5	-4,5	0		16	180	180
120210	tao-trAttC-hay-382-001+02	5a	5	-1,3	-1,5	9400	8	0	20	up	-15,5	-4,5	0		16	180	
120210	tao-trAttC-hay-382-001+03	3a	3	-1,3	-1,5	9161	9	0	20	up	-15,5	-4,5	0		16	270	180
120210	tao-trAttC-hay-382-001+03	5a	5	-1,3	-1,5	9400	9	0	20	up	-15,5	-4,5	0		16	270	240-270
120214	tao-trAttC-hay-384-001+01	2a	2	-2	-1,3	9462	8	0	20	right	-15	9	0		8	270	270
120215	tao-trAttC-hay-385-001+02		2	-2	-0,8	9537	excluded, not enough trials										
120215	tao-trAttC-hay-385-001+02		2	-2	-0,8	9537	excluded, not enough trials										
120216	tao-trAttC-hay-386-001+01	3a	3	-2	-0,5	9100	8	0	20	up	-17	5	0	all	16	240	210-240
120216	tao-trAttC-hay-386-001+01	3b	3	-2	-0,5	9100	mu	0						16	16		
120216	tao-trAttC-hay-386-001+02	1a	1	-2	-0,5	9196	8	0	20	up	-17	5	0		16	0	0-60
120216	tao-trAttC-hay-386-001+02	1b	1	-2	-0,5	9196	8	0	20	up	-17	5	0		16	0	330-0
120222	tao-trAttC-hay-389-001+01	2a	2	-2,2	-0,8	9636	9	0	20	up	-16	4	0		16	300	300
120222	tao-trAttC-hay-389-001+02	1a	1	-2,2	-0,8	9358	8	0	20	up	-16	4	1	16	16	300	300
120222	tao-trAttC-hay-389-001+02	5b	5	-2,2	-0,8	9269	8	0	20	up	-16	4	2		16	300	
120223	tao-trAttC-hay-390-001+01	3a	3	-2,2	-0,5	9200	8	0	20	right	-22	8	0		16	210	180-240
120223	tao-trAttC-hay-390-001+01	5a	5	-2,2	-0,5	9200	9	0	20	right	-22	8	0		16	210	210-240
120223	tao-trAttC-hay-390-001+02	1a	1	-2,2	-0,5	9200	8	0	20	right	-22	8	0		16	210	210
120223	tao-trAttC-hay-390-001+02	2a	2	-2,2	-0,5	9200	9	0	20	right	-22	8	0		16	210	
120223	tao-trAttC-hay-390-001+02	5b	5	-2,2	-0,5	9200	8	0	20	right	-22	8	0		16	210	210
120224	tao-trAttC-hay-391-001+01	1a	1	-2	-1	9522	9	0	20	up	-16	5	0		16	30	30
120224	tao-trAttC-hay-391-001+01	1b	1	-2	-1	9522	8	0	20	up	-16	5	0		16	30	30-60
120224	tao-trAttC-hay-391-001+01	2a	2	-2	-1	9643	8	0	20	up	-16	5	0		16	30	0-30
120224	tao-trAttC-hay-391-001+01	3a	3	-2	-1	9345	mu										
120309	tao-trAttC-hay-395-001+01	2a	2	+0.5	+0.7	9765	8	0	20	down	-12	-5	0		4	300	270-300
120320	tao-trAttC-hay-396-001+01	4b	4	+1.2	+1.5	9665	8	0	15	down	-3	-3			4	300	300
120320	tao-trAttC-hay-396-001+02	4a	4	+1.2	+1.5	9665	9	0	15	down	-3	-3	0		8	300	270-300
120321	tao-trAttC-hay-397-001+01	1a	1	+1.5	+2.0	9600	8	0	20	down	-10	0	0		8	210	210-240
120321	tao-trAttC-hay-397-001+01	2a	2	+1.5	+2.0	9629	8	0	20	down	-10	0	0		8	210	180-240
120321	tao-trAttC-hay-397-001+02	4a	4	+1.5	+2.0	9549	8	0	20	down	-8	-5	0		8	300	120
120322	tao-trAttC-hay-398-001+01	1a	1	+2.0	+1.5	9827	9	0	15	down	-5	-4	0	all	8	0	0-60
120322	tao-trAttC-hay-398-001+01	5a	5	+2.0	+1.5	10204	8	0	15	down	-5	-4	0		8	0	330-0
120322	tao-trAttC-hay-398-001+02	1a	1	+2.0	+1.5	9800	8	0	15	down	-5	-4	0		8		
120322	tao-trAttC-hay-398-001+02	3a	3	+2.0	+1.5	9824	8	0	15	down	-5	-4	0		8	0	180-210
120322	tao-trAttC-hay-398-001+02	5a	5	+2.0	+1.5	10000	8	0	15	down	-5	-4	0		8		
120323	tao-trAttC-hay-399-001+01	5a	5	+1.0	+1.5	9280	8	0	20	right	-12	-10	0	16	16	270	210-270
120327	tao-trAttC-hay-400-001+01	3a	3	+0.0	-1	9979	8	0	15	right	-5	-10	0	16	16	300	270-300
120327	tao-trAttC-hay-400-001+02	4a	4	+0.0	-1	10329	8	0	15	right	-5	-10	0	16	16	300	
120327	tao-trAttC-hay-400-001+02	5a	5	+0.0	-1	9829	9	0	15	right	-5	-10	0	16	16	300	
120328	tao-trAttC-hay-401-001+01	2a	2	-0,5	-1	10948	8	0	15	right	-5	-10	0	16	16	300	

120328	tao-trAttC-hay-401-001+01	3b	3	-0,5	-1	10081	8	0	15	right	-4,5	-9	0	16	16	60	
120328	tao-trAttC-hay-401-001+01	4a	4	-0,5	-1	10516	8	0	15	right	-4,5	-9	0		16	60	
120328	tao-trAttC-hay-401-001+01	4b	4	-0,5	-1	10516	8	0	15	right	-4,5	-9	0	all	16	60	
120328	tao-trAttC-hay-401-001+02	5a	5	-0,5	-1	10556	9	0	15	right	-1,5	-8	0	16	16	0	0-60
120328	tao-trAttC-hay-401-001+03	5a	5	-0,5	-1	10300	9	0	15	right	-1,5	-8	0	16	16	0	330-0
120329	tao-trAttC-hay-402-001+01	2a	2	-0,7	-0,5	10709	8	0	20	down	-10	-7,5	0	16	16	270	210-270
120329	tao-trAttC-hay-402-001+02	2b	2	-0,7	-0,5	10709	8	0	15	right	-4,5	-10	0	16	16	90	90-120
120329	tao-trAttC-hay-402-001+02	3a	3	-0,7	-0,5	10876	8	0	15	right	-4,5	-10	0	8	16	90	90-120
120329	tao-trAttC-hay-402-001+03	5a	5	-0,7	-0,5	11151	8	0	15	right	-2,5	-9,5	0		16	30	240-330
120330	tao-trAttC-hay-403-001+01	5b	5	-1	+0.0	10180	9	0	20	down	-10	0	0		16	90	60-90
120331	tao-trAttC-hay-404-001+01	3a	3	+2.5	+1.0	9557	8	0	15	down	-10	0	0	16	16	0	330-0
120331	tao-trAttC-hay-404-001+01	4a	4	+2.5	+1.0	11101	8	0	15	down	-10	0	0		16	0	
120331	tao-trAttC-hay-404-001+01	5a	5	+2.5	+1.0	10914	8	0	15	down	-10	0	0		16	0	330-2
120401	tao-trAttC-hay-405-001+01	2a	2	+1.5	+1.5	10234	8	0	15	down	-5	1	0	4--8	16	30	30
120401	tao-trAttC-hay-405-001+02	4a	4	+1.5	+1.5	11416	8	0	15	down	-4	0	0	all	16	300	270-330
120402	tao-trAttC-hay-406-001+01	3b	3	-1	-1	10909	8	0	20	right	-2	-9,5	0	16	16	30	330-60
120402	tao-trAttC-hay-406-001+01	5b	5	-1	-1	10946	8	0	20	right	-2	-9,5	0	all	16	30	0-30
120402	tao-trAttC-hay-406-001+02	3a	3	-1	-1	10909	9	0	20	right	-2	-9,5	0		16	30	30-60
120402	tao-trAttC-hay-406-001+02	5a	5	-1	-1	10946	8	0	20	right	-2	-9,5	0		16	30	0-30
120403	tao-trAttC-hay-407-001+01	1a	1	-1,3	-1	10338	8	0	20	down	-9,5	-5	0	8	8	60	30-120
120403	tao-trAttC-hay-407-001+01	5a	5	-1,3	-1	10314	8	0	20	down	-9,5	-5	0	8--16	8	60	180-240
120403	tao-trAttC-hay-407-001+02	1a	1	-1,3	-1	10338	8	0	20	down	-9,5	-5	0		8	60	
120404	tao-trAttC-hay-409-001+02	2a	2	-1	-0,5	11897	8	0	15	right	-5	-10	0	all	16	330	270-330
120404	tao-trAttC-hay-409-001+02	2b	2	-1	-0,5	11897	8	0	15	right	-5	-10	0	16	16	330	300-330
120404	tao-trAttC-hay-409-001+02	5a	5	-1	-0,5	11400	8	0	20	right	-5	-10	0	16	16	330	270-330
120405	tao-trAttC-hay-410-001+01	4a	4	-1,5	-1,5	12052	8	0	20	right	-8	-9,5	0	16	16	30	30

Additional supplementary materials 3: Supplementary data

S1 Data. The data presented in Fig 2.

Note:
Fig2PSTH_monkeyH.txt contains the values for the population average PSTHs for monkey H in Figure 2A
Fig2PSTH_monkeyE.txt contains the values for the population average PSTHs for monkey E in Figure 2B
Fig2MIvalues_monkeyH.txt contains the modulation index values for monkey H in Figures 2C and 2D
Fig2MIvalues_monkeyE.txt contains the modulation index values for monkey E in Figures 2E and 2F

Fig2PSTH_monkeyE:

	Time_(ms)	P_attend-in	P_attend-out	AP_attend-in	AP_attend-out	Simple-saccade
1	-295	6.8643	5.9907	6.2654	5.9183	6.0491
2	-285	6.9427	6.0637	6.1081	5.8055	6.1316
3	-275	6.8419	6.5777	5.9522	5.907	6.1086
4	-265	6.9823	6.7363	6.1045	5.2305	6.0633
5	-255	7.0865	7.047	6.1802	5.3909	6.5502
6	-245	6.8073	7.2828	5.787	5.3506	6.5601
7	-235	6.7682	7.5907	6.1009	4.6276	6.693
8	-225	7.007	7.8449	6.7315	4.7898	7.3621
9	-215	7.184	8.2418	6.6224	5.1015	7.4073
10	-205	7.4827	8.4272	6.8995	5.1312	6.9309
11	-195	7.926	8.6257	7.5175	5.2571	6.9887
12	-185	8.2704	8.1686	7.3284	5.8131	6.7593
13	-175	8.1043	7.8688	6.8705	6.1595	6.0916
14	-165	8.1921	7.9802	6.7981	6.3029	5.9605
15	-155	7.5422	8.1234	6.9047	6.016	5.9973
16	-145	7.7169	7.0859	7.1163	5.7055	6.0143
17	-135	7.5237	7.1721	6.6313	5.5733	6.1687
18	-125	7.3994	7.1247	6.3553	5.7005	6.4877
19	-115	6.9736	6.7173	6.1579	5.6512	6.6874
20	-105	7.542	6.5949	6.2025	6.1831	6.6807
21	-95	7.1449	7.4133	5.1948	6.404	6.5904
22	-85	7.1767	7.5083	5.0985	6.2615	6.5843
23	-75	7.1531	7.8896	5.3331	6.278	6.6385
24	-65	6.9939	7.6797	5.3328	6.1895	6.765
25	-55	6.7789	8.0322	4.4593	6.1144	7.037
26	-45	7.2952	7.807	4.9024	5.9858	6.6931
27	-35	6.5997	7.1869	4.7984	5.9186	6.6186
28	-25	7.1126	7.1784	5.2464	5.8133	6.6489
29	-15	7.8864	7.4067	6.3424	6.1164	6.572
30	-5	8.823	7.5038	7.4117	6.7671	6.4818
31	5	13.2635	12.1245	10.3385	10.6774	6.5758
32	15	24.1653	24.4266	16.5104	16.5346	7.1724
33	25	38.4962	38.8245	20.3848	20.9588	7.561
34	35	53.4892	56.3231	23.054	23.0868	7.9484
35	45	67.9428	70.0988	23.3376	23.5945	8.3192
36	55	77.4654	79.4004	21.8201	20.9516	8.6306
37	65	78.9911	79.6599	17.147	15.9554	8.4085
38	75	75.7192	74.4635	13.6187	12.2389	8.4724
39	85	70.5429	66.6595	11.0649	10.1639	8.6221
40	95	64.7104	60.7728	10.7565	9.8276	8.2949
41	105	60.5882	54.9879	9.8739	9.1044	8.1156
42	115	58.3844	50.4202	10.0392	9.1046	7.6174
43	125	56.8897	48.6988	10.742	8.2565	7.0413
44	135	56.5921	47.2485	10.1219	8.2507	6.3539
45	145	56.1362	45.7586	9.9032	7.4872	5.8218
46	155	54.8559	46.8613	10.1663	7.3394	5.807
47	165	54.2857	48.4441	10.059	7.0473	5.8482
48	175	54.3667	47.8982	8.8947	7.4957	5.5842

49	185	53.2471	48.015	9.6651	7.587	5.5152
50	195	52.8301	49.3076	9.9622	8.4741	6.0539
51	205	52.6099	46.9615	9.9816	8.5339	6.32
52	215	52.3183	43.8884	10.2324	9.3969	6.4275
53	225	51.3302	44.5729	10.9806	9.2387	6.8207
54	235	50.7501	42.1133	10.7815	9.8969	7.2764
55	245	50.0488	40.9146	11.1418	10.2518	7.2709
56	255	48.5066	41.1559	10.7063	10.6116	6.9037
57	265	48.4299	41.5955	9.9572	10.1205	7.0101
58	275	47.7662	40.7769	9.899	10.4532	6.992
59	285	47.1147	42.2652	9.6176	9.4837	6.7644
60	295	47.029	42.6726	9.2691	8.7517	6.8169
61	305	48.9707	43.3173	10.0676	8.6545	6.8405
62	315	47.8292	43.1471	10.4833	8.5973	7.1827
63	325	47.4229	43.1757	11.2833	8.1862	7.12
64	335	47.5508	41.9683	10.9855	8.7784	7.4115
65	345	47.3137	40.6478	10.4328	8.3365	7.4647
66	355	46.8646	39.543	9.5245	8.0955	8.1269
67	365	47.2756	40.2589	9.4628	7.7351	7.9735
68	375	47.0865	38.8507	8.6166	7.8718	7.9032
69	385	47.2771	38.5805	9.0652	7.1582	7.6416
70	395	46.6289	39.1221	8.6229	7.6873	7.703
71	405	45.3316	38.9341	8.4959	7.3922	7.6908
72	415	45.1359	37.4904	8.5845	7.2607	7.7045
73	425	45.568	38.5132	8.4755	7.2138	8.0479
74	435	44.8283	38.9639	8.3928	7.6331	8.1293
75	445	45.2114	37.4274	8.932	7.1595	8.4795
76	455	45.1588	36.5565	8.6039	7.5514	8.1139
77	465	43.9859	36.9925	7.9016	8.4888	7.7816
78	475	42.4697	35.8865	7.5611	8.8249	7.4721
79	485	42.5969	35.7472	7.4979	9.1501	7.2867
80	495	40.9023	37.5231	7.3863	9.341	6.9423
81	505	41.2752	38.7126	8.392	8.726	6.6854
82	515	41.2806	38.8393	8.7114	8.1653	6.8244
83	525	41.9506	38.6504	8.7075	7.7588	6.98
84	535	42.1627	39.042	8.7384	7.4309	6.6123
85	545	43.3088	37.922	9.5248	7.0487	6.3215
86	555	42.917	36.5581	9.0243	7.7574	6.0025
87	565	43.9043	36.8331	9.1915	8.301	6.076
88	575	44.8165	37.6062	9.0221	8.0828	5.7829
89	585	44.6293	36.9466	8.9821	7.8369	5.982
90	595	43.9262	36.7414	8.068	7.8331	5.796

Fig2PSTH_monkeyH:

	Time_(ms)	P_attend-in	P_attend-out	AP_attend-in	AP_attend-out	Simple-saccade
1	-295	12.1429	11.5615	10.4756	12.3397	10.728
2	-285	11.4081	11.6179	10.5358	12.7293	11.2092
3	-275	11.3363	11.1535	11.1676	12.24	11.1363
4	-265	10.9324	11.2235	11.0658	11.9961	11.5609
5	-255	10.7607	11.2145	11.082	12.6638	11.7394
6	-245	10.715	10.0289	12.05	12.6839	11.687
7	-235	11.3207	10.1617	12.8609	12.4806	11.6618
8	-225	10.8928	10.9883	12.5282	12.4542	12.1024
9	-215	10.965	11.4531	12.7668	13.1201	12.0943
10	-205	10.9802	11.5427	12.5275	12.4552	12.2439
11	-195	11.1186	11.9435	12.2353	12.6009	12.7301
12	-185	11.902	12.3394	12.003	12.8618	12.6851
13	-175	12.2422	12.0798	12.0597	13.0299	12.3712
14	-165	12.9166	11.5936	11.8977	12.808	12.8556
15	-155	12.6147	11.7621	11.9833	13.1112	13.1231
16	-145	12.9501	11.6425	11.7107	12.7087	12.5384

17	-135	11.9641	11.1321	11.2878	12.5772	12.4268
18	-125	11.8054	12.0221	11.0975	12.0954	12.5258
19	-115	11.7338	11.2951	11.4888	11.5186	12.0528
20	-105	12.2882	10.853	12.0475	11.1021	12.5294
21	-95	12.1085	10.8797	11.9159	10.6637	11.917
22	-85	12.4457	11.1705	11.7246	10.2936	11.649
23	-75	12.4034	10.3263	11.839	10.7664	11.5439
24	-65	11.8128	10.7719	11.3361	11.3844	11.5576
25	-55	11.6828	10.8981	11.3886	12.1968	10.4235
26	-45	13.3484	12.129	13.2308	14.4701	11.9476
27	-35	14.6688	14.9085	15.7362	16.6901	14.4057
28	-25	17.2326	17.7141	17.9809	18.3258	16.6822
29	-15	19.8943	19.8044	20.1627	19.5797	18.5301
30	-5	21.2299	21.2804	21.5919	20.3215	20.6558
31	5	23.0654	24.4708	23.1691	22.0593	19.9806
32	15	31.644	30.8017	28.1785	26.0435	17.5046
33	25	43.7739	40.8324	29.9506	28.1984	15.5098
34	35	54.8218	51.2405	30.7758	29.172	14.4719
35	45	67.7425	63.0609	32.3068	30.3759	13.1266
36	55	78.3006	73.144	33.0155	30.4428	12.7034
37	65	83.448	78.0107	29.5549	26.9793	12.8588
38	75	84.2085	81.0694	28.0091	25.0639	11.6375
39	85	86.4664	84.098	28.7557	24.8147	10.0267
40	95	85.2437	84.2451	28.7931	25.8458	9.0967
41	105	85.5129	80.9804	28.8485	24.9205	8.1545
42	115	82.5523	79.6729	28.0116	24.8873	7.6339
43	125	79.7668	75.3402	28.9601	26.0246	7.7996
44	135	76.1499	71.2112	28.383	26.1323	8.4228
45	145	75.0806	68.5873	27.7023	26.1612	9.0417
46	155	72.8722	68.587	27.0512	26.2048	10.4076
47	165	73.0604	65.6593	27.5633	26.3833	11.3047
48	175	71.9665	63.8911	27.2919	26.2677	11.9577
49	185	70.2321	62.2052	27.3172	27.0047	12.5888
50	195	68.5066	59.8275	28.4286	26.5811	12.8145
51	205	67.2255	57.3243	28.8307	27.0591	12.6929
52	215	65.577	57.1259	29.4792	27.2909	12.1719
53	225	64.0531	56.5684	29.9381	27.6181	12.0455
54	235	63.0211	55.7627	31.4293	27.5571	11.184
55	245	62.9899	57.5001	31.3329	27.5216	10.6047
56	255	62.2419	57.764	30.7269	26.4665	9.4405
57	265	60.2507	57.5727	29.6478	25.1994	8.999
58	275	61.0187	58.2816	28.4025	23.7817	8.0719
59	285	60.5248	58.3406	27.3268	22.3885	7.3311
60	295	60.0672	57.977	26.4865	21.576	6.9751
61	305	59.5028	57.7171	26.7879	20.7048	7.2499
62	315	59.8991	57.0466	26.8603	21.2176	7.5582
63	325	59.616	56.002	27.446	20.8891	8.1673
64	335	60.4979	55.365	26.3832	20.4021	8.7779
65	345	61.77	54.8385	26.9204	19.4792	9.2877
66	355	62.5807	54.5521	25.3455	20.0542	9.9165
67	365	63.7091	54.1162	24.6518	19.3076	10.3193
68	375	64.2047	53.8163	24.2839	19.7445	10.3569
69	385	65.2001	53.6106	23.9144	20.7237	10.5672
70	395	64.4392	52.4517	22.4566	21.5523	10.6995
71	405	63.5781	51.1137	23.1882	21.2288	10.9052
72	415	63.0292	50.1711	23.4376	20.9423	10.811
73	425	61.3393	49.6375	22.5479	21.0596	10.8136
74	435	60.8051	49.7699	23.5172	20.3161	10.7349
75	445	60.5636	49.6264	24.0416	19.5493	10.2185
76	455	60.7205	50.4092	23.4962	19.4051	9.3384
77	465	60.4047	50.526	23.5393	19.7046	8.8898
78	475	60.1702	51.0291	24.367	18.7833	8.6895
79	485	59.5418	50.8747	24.1428	19.0287	8.4713

80	495	58.73	50.4487	24.5639	19.6488	8.5437
81	505	58.2412	50.2951	24.1483	19.9825	8.7452
82	515	56.3278	50.8432	23.589	19.9455	8.5183
83	525	56.1956	49.8552	23.2991	20.3266	8.332
84	535	55.2857	50.7582	22.5046	19.2444	8.4256
85	545	54.926	50.9781	22.4102	18.3135	8.5048
86	555	54.2172	51.3365	22.7945	18.4696	8.2536
87	565	56.2641	51.3232	22.9243	18.4819	8.4425
88	575	56.4323	51.6389	23.0428	18.5023	8.8724
89	585	57.5696	50.8237	23.8592	19.8267	8.6968
90	595	57.6001	50.318	22.9096	20.2621	8.263

Fig2MIvalues_monkeyE:

	MIPreferred_monkeyE	MIAntiPreferred_monkeyE
1	0.20792	0.058824
2	-0.038462	-0.1039
3	0.027104	0.056122
4	0.055497	0.35714
5	0.14228	0.35
6	0.07907	-0.023622
7	-0.011765	0.15315
8	0.067692	0.090274
9	0.04142	0.12583
10	0.16753	0.14114
11	0.18798	0.26538
12	0.08169	0.018182
13	0.11193	0.12727
14	0.12	-0.090909
15	0.12842	0.62712
16	0.041053	-0.097087
17	0.010249	-0.020013
18	0.067114	0.29412
19	0.028728	-0.38558
20	0.07064	0.038627
21	0.051237	0.16263
22	0.12409	0.14286
23	0.22171	-0.047619
24	0.092199	-0.0837
25	0.039427	-0.077145
26	-0.014374	-0.21212
27	0.002798	-0.16493
28	0.27184	0.23077
29	0.17486	0.23849
30	0.036578	-0.016949
31	0.057239	-0.025641
32	0.0076336	0.22857
33	0.036739	-0.069444
34	0.067215	-0.22353
35	0.037736	-0.083333
36	0.023041	-0.0011751
37	-0.19199	-0.063415
38	-0.043956	0.0013004
39	0.083842	0.056338
40	0.09671	-0.18182
41	0.05914	0.095344
42	0.044444	0.21771
43	-0.15267	0.28205
44	0.13407	0

Fig2MIvalues_monkeyH:

	MIPreferred	MIAntiPreferred
1	0.59184	0.11111
2	0.0081566	0.40187
3	0.036005	0.014925
4	0.07109	0.11064
5	-0.038223	0.13043
6	0.055249	-0.015385
7	0.023228	0.091703
8	0.063142	0.20334
9	-0.0036765	-0.13208
10	0.042983	0.14835
11	0.067961	-0.058824
12	0.0063008	0.0069572
13	0.017507	0.26437
14	0.11321	0
15	0.077956	0.12444
16	-0.027027	0.027027
17	0.04	0.02509
18	0.1049	-0.043643
19	-0.01002	-0.034982
20	-0.013477	-0.0301
21	0.15207	0.21892
22	0.074642	0.10386
23	0.12814	0.21916
24	0.074634	0.11307
25	-0.0097989	0.19728
26	0.10549	0.013874
27	0.023853	-0.038407
28	-0.076923	-0.041667
29	0.019524	0.049096
30	-0.0040699	0.083871
31	0.051903	0.10345
32	0.0048867	0.015625
33	0.036743	-0.042821
34	0.060878	0.07563
35	-0.049923	0.087452
36	-0.010231	0.19622
37	0.045685	0.030303
38	-0.039834	-0.061453
39	0.07642	-0.10181
40	0.065102	1
41	0.034939	0.062189
42	0.06008	0.053892
43	0.12886	0.092593
44	0.084639	0.065741
45	0.042518	0.027257

46 0.060956 0.068966

S2 Data. The data presented in Fig 3.

Note:
Fig3PSTH_monkeyH.txt contains the values for the population average PSTHs for monkey H in Figure 3A
Fig3PSTH_monkeyE.txt contains the values for the population average PSTHs for monkey E in Figure 3B
Fig3MIvalues_monkeyH.txt contains the modulation index values for monkey H in Figure 3C
Fig3MIvalues_monkeyE.txt contains the modulation index values for monkey E in Figure 3D

Fig3PSTH_monkeyH:

	Time_(ms)	Attend-in	Simple-saccade
1	-295	11.4518	10.728
2	-285	11.4876	11.2092
3	-275	11.4812	11.1363
4	-265	11.4137	11.5609
5	-255	11.2676	11.7394
6	-245	11.5908	11.687
7	-235	11.7919	11.6618
8	-225	11.9095	12.1024
9	-215	12.0714	12.0943
10	-205	12.4413	12.2439
11	-195	12.5062	12.7301
12	-185	11.9943	12.6851
13	-175	11.8636	12.3712
14	-165	11.6359	12.8556
15	-155	11.3872	13.1231
16	-145	11.234	12.5384
17	-135	11.5155	12.4268
18	-125	11.4528	12.5258
19	-115	11.2976	12.0528
20	-105	11.3073	12.5294
21	-95	11.2955	11.917
22	-85	11.3825	11.649
23	-75	11.494	11.5439
24	-65	11.752	11.5576
25	-55	11.9717	10.4235
26	-45	13.2051	11.9476
27	-35	14.9251	14.4057
28	-25	16.838	16.6822
29	-15	18.7051	18.5301
30	-5	19.6043	20.6558
31	5	18.7901	19.9806
32	15	17.5608	17.5046
33	25	16.6105	15.5098
34	35	15.9552	14.4719
35	45	15.8533	13.1266
36	55	16.8379	12.7034
37	65	17.172	12.8588
38	75	16.9222	11.6375
39	85	16.8773	10.0267
40	95	16.7612	9.0967
41	105	16.4512	8.1545
42	115	16.4903	7.6339
43	125	16.5309	7.7996
44	135	16.2554	8.4228
45	145	16.7309	9.0417
46	155	16.4872	10.4076
47	165	15.9887	11.3047
48	175	15.7666	11.9577
49	185	15.591	12.5888
50	195	15.0154	12.8145
51	205	14.7174	12.6929
52	215	14.8583	12.1719
53	225	14.5276	12.0455
54	235	14.2113	11.184
55	245	13.7895	10.6047
56	255	13.4996	9.4405
57	265	12.7316	8.999
58	275	12.3094	8.0719
59	285	11.7077	7.3311
60	295	10.9823	6.9751
61	305	10.3358	7.2499
62	315	10.1912	7.5582
63	325	10.1259	8.1673
64	335	9.8775	8.7779
65	345	9.923	9.2877
66	355	10.0456	9.9165
67	365	10.1374	10.3193
68	375	10.4151	10.3569
69	385	10.7833	10.5672
70	395	11.0893	10.6995
71	405	11.0237	10.9052
72	415	11.2345	10.811
73	425	10.9757	10.8136
74	435	11.0735	10.7349
75	445	11.0134	10.2185
76	455	11.2289	9.3384
77	465	10.7574	8.8898
78	475	10.5471	8.6895
79	485	9.6931	8.4713
80	495	9.2936	8.5437

Fig3PSTH_monkeyE:

	Time_(ms)	Attend-in	Simple-saccade
1	-295	6.6472	6.0491
2	-285	6.7594	6.1316
3	-275	6.4685	6.1086
4	-265	6.4198	6.0633
5	-255	6.4725	6.5502
6	-245	6.6601	6.5601
7	-235	6.5333	6.693
8	-225	6.8262	7.3621
9	-215	6.7218	7.4073
10	-205	6.5813	6.9309
11	-195	6.3631	6.9887
12	-185	6.3833	6.7593
13	-175	6.1916	6.0916
14	-165	6.2639	5.9605
15	-155	6.5886	5.9973
16	-145	6.8516	6.0143
17	-135	6.9291	6.1687
18	-125	7.1972	6.4877
19	-115	7.2494	6.6874

20	-105	7.1947	6.6807
21	-95	6.9072	6.5904
22	-85	7.0546	6.5843
23	-75	6.7918	6.6385
24	-65	6.7183	6.765
25	-55	6.6669	7.037
26	-45	6.5429	6.6931
27	-35	6.4175	6.6186
28	-25	6.7661	6.6489
29	-15	6.919	6.572
30	-5	6.7686	6.4818
31	5	7.2084	6.5758
32	15	7.7801	7.1724
33	25	7.9965	7.561
34	35	8.3927	7.9484
35	45	8.8721	8.3192
36	55	9.4038	8.6306
37	65	9.8398	8.4085
38	75	10.2199	8.4724
39	85	10.5045	8.6221
40	95	10.5824	8.2949
41	105	9.6558	8.1156
42	115	8.6148	7.6174
43	125	7.7177	7.0413
44	135	6.8957	6.3539
45	145	6.3037	5.8218
46	155	6.5068	5.807
47	165	6.5004	5.8482
48	175	6.5412	5.5842
49	185	6.8463	5.5152
50	195	7.4954	6.0539
51	205	7.8047	6.32
52	215	8.5803	6.4275
53	225	9.0576	6.8207
54	235	9.1675	7.2764
55	245	9.0881	7.2709
56	255	9.1867	6.9037
57	265	8.8138	7.0101
58	275	8.4911	6.992
59	285	8.1794	6.7644
60	295	8.0584	6.8169
61	305	7.8894	6.8405
62	315	8.0673	7.1827
63	325	7.8739	7.12
64	335	8.0086	7.4115
65	345	8.0588	7.4647
66	355	7.9581	8.1269
67	365	7.516	7.9735
68	375	7.7432	7.9032
69	385	8.0627	7.6416
70	395	8.1075	7.703
71	405	8.4932	7.6908
72	415	8.9958	7.7045
73	425	9.2604	8.0479
74	435	9.1299	8.1293
75	445	9.0261	8.4795
76	455	8.8746	8.1139
77	465	8.2834	7.7816
78	475	7.7849	7.4721
79	485	7.5839	7.2867
80	495	7.6609	6.9423

Fig3MIvalues_monkeyH:

	MI_Attend-in_Vs_Simple-Saccade
1	1
2	0.33333
3	0.044833
4	-0.16663
5	-0.13299
6	-0.076336
7	-0.10122
8	0.18556
9	-0.55477
10	0.29831
11	0.16571
12	0.12085
13	1
14	-0.050346
15	0.5914
16	-0.14352
17	-0.030641
18	0.22558
19	-0.025918
20	0.22843
21	0.71542
22	-0.08731
23	0.80591
24	-0.098525
25	0.047191
26	0.14924
27	-0.023365
28	-0.18618
29	0.010473
30	0.17279
31	0.50871
32	0.18367
33	0.25517
34	0.38915
35	0.41962
36	-0.29399
37	0.039348
38	0.17062
39	0.099355
40	0.57576
41	0.2818
42	0.0454
43	0.114
44	0.23077
45	0.44216
46	0.64794

Fig3MIvalues_monkeyE:

	MI_Attend-in_Vs_Simple-Saccade
1	0.18455
2	0.14851
3	0.039753
4	-0.072411
5	-0.089109
6	0.093473
7	0.010989
8	0.051456

9	0.16364
10	-0.2053
11	-0.13043
12	0.26381
13	0.10818
14	-0.015773
15	-0.13106
16	0.089813
17	0.082517
18	0.21053
19	0.3042
20	0.2587
21	0.089494
22	-0.42717
23	-0.22555
24	0.15843
25	0.0044593
26	0.012048
27	-0.0074231
28	0.28405
29	0.13287
30	-0.05618
31	0.14591
32	0.04451
33	-0.0016849
34	0.071262
35	0.14897
36	0.24409
37	-0.035294
38	0.083478
39	0.15111
40	0.13852
41	0.027027
42	0.047486
43	-0.49677
44	-0.53982

S3 Data. The data presented in Fig 4.

Note:
Fig4PSTH_monkeyH.txt contains the values for the population average PSTHs for monkey H in Figure 4A
Fig4PSTH_monkeyE.txt contains the values for the population average PSTHs for monkey E in Figure 4B
Fig4MIvalues_monkeyH.txt contains the modulation index values for monkey H in Figures 4C,D
Fig4MIvalues_monkeyE.txt contains the modulation index values for monkey E in Figures 4E,F

Fig4PSTH_monkeyH:

	Time_(ms)	Attend-in	Attend-out	Simple-saccade
1	-295	11.4518	11.9827	10.728
2	-285	11.4876	11.7978	11.2092
3	-275	11.4812	11.7765	11.1363
4	-265	11.4137	11.5042	11.5609
5	-255	11.2676	11.7192	11.7394
6	-245	11.5908	11.4684	11.687
7	-235	11.7919	11.9624	11.6618
8	-225	11.9095	12.4152	12.1024
9	-215	12.0714	12.8407	12.0943
10	-205	12.4413	12.76	12.2439
11	-195	12.5062	12.7933	12.7301
12	-185	11.9943	12.6312	12.6851
13	-175	11.8636	12.4748	12.3712
14	-165	11.6359	12.415	12.8556
15	-155	11.3872	12.1764	13.1231
16	-145	11.234	12.2154	12.5384
17	-135	11.5155	12.1638	12.4268
18	-125	11.4528	12.3346	12.5258
19	-115	11.2976	12.3557	12.0528
20	-105	11.3073	12.7254	12.5294
21	-95	11.2955	12.6463	11.917
22	-85	11.3825	12.6727	11.649
23	-75	11.494	12.6505	11.5439
24	-65	11.752	12.3168	11.5576
25	-55	11.9717	12.3074	10.4235
26	-45	13.2051	13.6185	11.9476
27	-35	14.9251	15.7281	14.4057
28	-25	16.838	17.1761	16.6822
29	-15	18.7051	18.7173	18.5301
30	-5	19.6043	19.962	20.6558
31	5	18.7901	19.0231	19.9806
32	15	17.5608	17.1053	17.5046
33	25	16.6105	16.2872	15.5098
34	35	15.9552	15.9863	14.4719
35	45	15.8533	15.0264	13.1266
36	55	16.8379	14.9154	12.7034
37	65	17.172	14.6465	12.8588
38	75	16.9222	13.6597	11.6375
39	85	16.8773	12.3011	10.0267
40	95	16.7612	11.6608	9.0967
41	105	16.4512	11.0319	8.1545
42	115	16.4903	10.7706	7.6339
43	125	16.5309	10.9795	7.7996
44	135	16.2554	11.2042	8.4228
45	145	16.7309	11.0155	9.0417
46	155	16.4872	11.4639	10.4076
47	165	15.9887	11.832	11.3047
48	175	15.7666	12.0892	11.9577
49	185	15.591	12.0405	12.5888
50	195	15.0154	12.4861	12.8145

51	205	14.7174	13.171	12.6929
52	215	14.8583	13.0928	12.1719
53	225	14.5276	12.7933	12.0455
54	235	14.2113	12.7198	11.184
55	245	13.7895	12.3831	10.6047
56	255	13.4996	11.2171	9.4405
57	265	12.7316	10.6032	8.999
58	275	12.3094	10.2022	8.0719
59	285	11.7077	9.9963	7.3311
60	295	10.9823	9.3598	6.9751
61	305	10.3358	9.026	7.2499
62	315	10.1912	8.681	7.5582
63	325	10.1259	8.4872	8.1673
64	335	9.8775	8.1278	8.7779
65	345	9.923	8.2983	9.2877
66	355	10.0456	8.4438	9.9165
67	365	10.1374	8.8727	10.3193
68	375	10.4151	9.1382	10.3569
69	385	10.7833	9.5917	10.5672
70	395	11.0893	9.8954	10.6995
71	405	11.0237	10.2827	10.9052
72	415	11.2345	10.3578	10.811
73	425	10.9757	10.1934	10.8136
74	435	11.0735	10.1678	10.7349
75	445	11.0134	10.2026	10.2185
76	455	11.2289	10.4017	9.3384
77	465	10.7574	10.3452	8.8898
78	475	10.5471	10.2031	8.6895
79	485	9.6931	9.616	8.4713
80	495	9.2936	8.9847	8.5437

Fig4PSTH_monkeyE:

	Time_(ms)	Attend-in	Attend-out	Simple-saccade
1	-295	6.6472	6.6631	6.0491
2	-285	6.7594	6.5231	6.1316
3	-275	6.4685	6.6156	6.1086
4	-265	6.4198	6.642	6.0633
5	-255	6.4725	6.6274	6.5502
6	-245	6.6601	6.7036	6.5601
7	-235	6.5333	6.8117	6.693
8	-225	6.8262	6.9909	7.3621
9	-215	6.7218	6.8842	7.4073
10	-205	6.5813	6.8382	6.9309
11	-195	6.3631	6.686	6.9887
12	-185	6.3833	6.6863	6.7593
13	-175	6.1916	6.6801	6.0916
14	-165	6.2639	6.6356	5.9605
15	-155	6.5886	6.7658	5.9973
16	-145	6.8516	6.8396	6.0143
17	-135	6.9291	6.5372	6.1687
18	-125	7.1972	6.334	6.4877
19	-115	7.2494	6.4056	6.6874
20	-105	7.1947	6.2785	6.6807
21	-95	6.9072	6.2594	6.5904
22	-85	7.0546	6.5267	6.5843
23	-75	6.7918	6.6197	6.6385
24	-65	6.7183	6.8254	6.765
25	-55	6.6669	7.0085	7.037
26	-45	6.5429	6.6829	6.6931
27	-35	6.4175	6.5372	6.6186
28	-25	6.7661	6.7878	6.6489
29	-15	6.919	6.734	6.572

30	-5	6.7686	6.6326	6.4818
31	5	7.2084	7.0821	6.5758
32	15	7.7801	7.7777	7.1724
33	25	7.9965	7.9323	7.561
34	35	8.3927	8.3153	7.9484
35	45	8.8721	8.8874	8.3192
36	55	9.4038	9.095	8.6306
37	65	9.8398	9.2681	8.4085
38	75	10.2199	9.6345	8.4724
39	85	10.5045	9.896	8.6221
40	95	10.5824	9.6585	8.2949
41	105	9.6558	9.1812	8.1156
42	115	8.6148	8.2455	7.6174
43	125	7.7177	7.5903	7.0413
44	135	6.8957	6.6869	6.3539
45	145	6.3037	6.216	5.8218
46	155	6.5068	6.0254	5.807
47	165	6.5004	6.0295	5.8482
48	175	6.5412	5.9211	5.5842
49	185	6.8463	6.2256	5.5152
50	195	7.4954	6.4991	6.0539
51	205	7.8047	6.9085	6.32
52	215	8.5803	7.5514	6.4275
53	225	9.0576	7.8899	6.8207
54	235	9.1675	8.0987	7.2764
55	245	9.0881	8.4481	7.2709
56	255	9.1867	8.6861	6.9037
57	265	8.8138	8.7158	7.0101
58	275	8.4911	8.6336	6.992
59	285	8.1794	8.3631	6.7644
60	295	8.0584	8.15	6.8169
61	305	7.8894	7.8575	6.8405
62	315	8.0673	7.5547	7.1827
63	325	7.8739	7.6964	7.12
64	335	8.0086	7.9964	7.4115
65	345	8.0588	8.0935	7.4647
66	355	7.9581	8.2146	8.1269
67	365	7.516	8.3196	7.9735
68	375	7.7432	8.0215	7.9032
69	385	8.0627	8.0136	7.6416
70	395	8.1075	8.0841	7.703
71	405	8.4932	8.392	7.6908
72	415	8.9958	8.7001	7.7045
73	425	9.2604	9.031	8.0479
74	435	9.1299	9.0852	8.1293
75	445	9.0261	8.9357	8.4795
76	455	8.8746	8.7573	8.1139
77	465	8.2834	8.2551	7.7816
78	475	7.7849	8.4226	7.4721
79	485	7.5839	8.3619	7.2867
80	495	7.6609	8.3591	6.9423

Fig4MIvalues_monkeyH:

	MI_Attend-in_Vs_Attend-out	MI_Attend-out_Vs_Simple-Saccade
1	0.64858	1
2	0.049668	0.28844
3	0.18042	-0.1367
4	0.11086	-0.27246
5	-0.02605	-0.10731
6	-0.051765	-0.024668
7	-7.2438e-05	-0.10115
8	0.036436	0.15014
9	-0.25	-0.35385
10	0.088058	0.21592
11	0.16239	0.003413
12	0.040986	0.080266
13	0	1
14	0.3942	-0.4359
15	0.51899	0.10448
16	0.17005	-0.3061
17	-0.055375	0.024776
18	0.041609	0.18571
19	0.28172	-0.3054
20	0.15001	0.081197
21	0.64636	0.12846
22	-0.16638	0.080238
23	0.56575	0.44141
24	-0.033969	-0.064773
25	0.12301	-0.076264
26	0.14656	0.0027302
27	0.028424	-0.051754
28	-0.16832	-0.018445
29	0.12583	-0.11551
30	0.026942	0.14653
31	0.30901	0.23695
32	0.27921	-0.1007
33	0.066955	0.19149
34	0.22856	0.17628
35	0.10811	0.32632
36	-0.026142	-0.26992
37	0.0023145	0.037037
38	0.16773	0.0029674
39	0.12947	-0.030508
40	0.17785	0.4433
41	0.092154	0.1947
42	0.11465	-0.069612
43	0.038419	0.075916
44	0.11669	0.11723
45	0.21672	0.24933
46	0.66038	-0.021739

Fig4MIvalues_monkeyE:

	MI_Attend-in_Vs_Attend-out	MI_Attend-out_Vs_Simple-Saccade
1	0.104	0.082126
2	0.067485	0.081851
3	-0.029204	0.068878
4	0.12821	-0.19877
5	0.125	-0.21175
6	0.063063	0.03059
7	8.3267e-17	0.010989
8	0.064102	-0.012688
9	0.20962	-0.047619
10	-0.12145	-0.085989
11	-0.28926	0.16505
12	0.14258	0.12597
13	-0.011537	0.11957
14	0.3	-0.31429
15	0.29412	-0.4094
16	-0.028405	0.11792
17	-0.077294	0.1588
18	0.044927	0.16718
19	0.012048	0.29322
20	0.31646	-0.062907
21	0.033058	0.056604
22	-0.34177	-0.1
23	0.14176	-0.35593
24	-0.042394	0.19949
25	-0.022291	0.026747
26	0.16584	-0.1541
27	-0.024619	0.017199
28	0.11864	0.17117
29	0.24276	-0.11356
30	0.081397	-0.13695
31	0.13078	0.015431
32	-0.00094607	0.045455
33	-0.10848	0.10682
34	0.13728	-0.066667
35	0.14897	0
36	0.032393	0.21339
37	0.09024	-0.12514
38	0.058872	0.024728
39	0.30997	-0.16667
40	0.067354	0.071838
41	0.16014	-0.13369
42	0.21176	-0.16594
43	0.016949	-0.50943
44	-0.18367	-0.39535

S4 Data. The data presented in Fig 5:

Note:
Fig5DIvalues_monkeyH.txt contains the direction-tuning index values for monkey H in Figures 5A and 5B
Fig5DIvalues_monkeyE.txt contains the direction-tuning index values for monkey E in Figures 5C and 5D
HeldOutTrials_DIvalues_monkeyH.txt contains the direction-tuning index values for monkey H reported in the text using only the held-out trials
HeldOutTrials_DIvalues_monkeyE.txt contains the direction-tuning index values for monkey H reported in the text using only the held-out trials

Fig5DIvalues_monkeyH:

	DIAttendIn_PvsAP	DIAttendOut_PvsAP
1	-0.40659	0.034483
2	0.15789	0.1276
3	-0.067521	-0.13559
4	-0.17726	-0.26154

5	0.028902	0.0097561
6	-0.01179	0.064962
7	-0.025086	0.019685
8	-1.1211e-16	0.081413
9	0.33333	-0.62832
10	0.099778	-8.2239e-17
11	0.041667	-0.048456
12	-0.00051467	-0.031752
13	-0.26316	-0.11325
14	0.38462	0.11765
15	-0.0625	-0.013333
16	0.15	-0.084681
17	0.046729	0.03936
18	0.10128	0.088353
19	-0.02439	0.053763
20	0.018182	0.042025
21	-0.0045366	0.11374
22	-0.064669	0.14132
23	0.069909	0.013398
24	0.19192	-0.18495
25	-0.012876	-0.034
26	0.093525	0.093539
27	-0.070352	0.010638
28	0	0.084746
29	0.035294	0.080808
30	0.028953	-0.013453
31	0.088172	-0.038082
32	0.017241	0.104
33	-0.00061237	0.11504
34	0.069359	0.16176
35	0.02439	0.090909
36	0.096774	0.14754
37	0.034655	0.0054945
38	-0.11864	0.03537
39	0.017594	-0.047715
40	-0.15385	0.14286
41	0.097276	0.058252
42	-0.1011	-0.10852
43	-0.034301	0.19325
44	0.049236	-0.067894
45	0.073684	0.036429
46	-0.11542	-0.13208

Fig5DIvalues_monkeyE:

	DIAttendIn_PvsAP	DIAttendOut_PvsAP
1	0.059289	-0.034965
2	-0.12853	-0.04451
3	-0.040971	-0.047819
4	-0.16024	0.35484
5	-0.54	-0.066667
6	0.018834	-0.020576
7	-0.073171	-0.16088
8	0.033708	-0.038298
9	-0.043478	-0.6
10	-0.28302	-0.28467
11	-0.025641	-0.67939
12	-0.39433	-0.011765
13	-0.041913	0.066128
14	-0.18919	-0.39241
15	-0.20988	-0.31343
16	0.1209	0.09589
17	0.074257	0.11852
18	0.218	0.14108
19	0.018868	0.13982
20	0.2911	-0.016641
21	0	0.04
22	-0.78512	0.44444
23	0.058268	0.47368
24	0.022457	-0.097749
25	0.060939	0.011152
26	0.1086	0.16542
27	-1.1358e-16	-0.10569
28	0.013193	0
29	-0.19308	-0.034483
30	0.030794	0.08982
31	0.04	-0.14868
32	-0.11111	0.028986
33	-0.030268	-0.086076
34	0.0040346	-0.028571
35	0.46358	-0.55556
36	0.11392	-0.082353
37	0.02439	0.023522
38	0.11063	-0.16883
39	-0.029412	-0.24138
40	0.11888	0.35275
41	0	0.018182
42	-0.62025	0.043478
43	-0.2381	0.6
44	-0.41818	0.3913

HeldOutTrials_DIvalues_monkeyH:

	DIAttendIn_PvsAP	DIAttendOut_PvsAP
1	-0.68421	-1
2	0.17757	0.090909
3	0.087799	0.24611
4	0.17391	0.37143
5	-0.10414	-0.042017
6	-0.069054	0.081511
7	-0.04644	-0.012061
8	-0.14146	0.11628
9	1	1
10	-0.10942	-0.2691
11	-0.018182	0.013699
12	-0.017544	-0.022288
13	0.41176	0.029412
14	0.51899	-0.093525
15	-1	-0.17647
16	0.052632	0.16667
17	-0.093562	-0.11558
18	0.0027248	-0.14826
19	-0.5	-0.044177
20	-0.10828	-0.093333
21	-0.13043	-0.30165
22	-0.17073	0.016949
23	0.10638	-0.12821
24	0.30769	0.29412
25	-0.03949	-0.13995
26	0.083333	-0.017341
27	-0.18462	-0.088083
28	-0.072797	0.07563
29	0.045783	-0.017964
30	-0.0090439	0.003337

31	0.031161	0.056604
32	0.0015504	0.02439
33	-0.022556	0.1954
34	0.125	0.20313
35	-0.33023	-0.21212
36	-0.12108	0.098592
37	0.058824	-0.057778
38	-0.12	-0.13514
39	-0.08835	0.074024
40	0.061453	0.17419
41	-0.031746	0.098039
42	0.032617	0.069807
43	-0.0082919	-0.074074
44	0.077966	-0.14953
45	0.093946	0.02958
46	0.18519	0.076923

HeldOutTrials_DIvalues_monkeyE:

	DIAttendIn_PvsAP	DIAttendOut_PvsAP
1	-0.133	0.028002
2	0.10141	0.062295
3	0.027523	0.05174
4	-0.35484	-0.1
5	0.53125	-0.29412
6	-0.02439	-0.12621
7	-0.11765	0.075795
8	0.034091	0.0079194
9	-0.043478	0.2973
10	0.052632	-0.8
11	-1	-1
12	0.31646	-0.089457
13	-0.18143	0.060847
14	0.28571	0.41176
15	0.33333	0.41176
16	0.22849	0.086614
17	0.09589	0.078498
18	0.10569	0.1236
19	-0.11789	0.24068
20	0.75	-0.1588
21	-1	-0.86667
22	1	0.74257
23	-0.066667	0.55556
24	0.017544	0.12088
25	0.023256	-0.004329
26	0.22222	0.61062
27	-0.09589	0.066667
28	-0.015625	-0.46667
29	0.2844	-0.058824
30	0.012412	0.2
31	-0.10698	0.21053
32	0.072423	-0.14655
33	0.050847	-0.026946
34	6.2172e-17	-0.13604
35	0.48148	0.42675
36	0.086876	0.018568
37	0.018739	-0.16129
38	-0.38776	-0.33119
39	-0.090909	0
40	0.16667	0.22222
41	-0.2	-0.04
42	0.65829	-0.47826
43	0.33333	0.45946
44	1	0.56522

S5 Data. The data presented in Fig 6

Note:
Each file contains the data for the PSTHs (A-D) and mean difference / confidence-bands (E-H).

Fig6APSTH_monkeyH:

	Time_(ms)	Preferred	Anti-preferred
1	-295	10.8977	12.089
2	-285	11.1259	11.8708
3	-275	11.3766	11.5292
4	-265	11.3496	11.3966
5	-255	11.5501	10.8345
6	-245	12.1066	10.9444
7	-235	12.1778	11.2943
8	-225	12.3774	11.4546
9	-215	12.2332	11.9179
10	-205	12.2384	12.7147
11	-195	12.1064	12.9404
12	-185	11.5609	12.5034
13	-175	10.9057	12.8654
14	-165	11.2328	12.2025
15	-155	11.1138	11.8228
16	-145	10.8973	11.7071
17	-135	11.4664	11.6502
18	-125	11.8695	11.0707
19	-115	11.6766	10.8474
20	-105	11.6553	10.9077
21	-95	11.5841	11.0119
22	-85	11.1708	11.535
23	-75	11.0086	11.919
24	-65	10.895	12.5199
25	-55	11.1046	12.6804
26	-45	12.2192	14.061
27	-35	14.1743	15.7038
28	-25	16.1167	17.5641
29	-15	18.3768	19.0211
30	-5	19.5915	19.6299
31	5	19.1716	18.3791
32	15	17.9945	16.9875
33	25	17.3827	15.7553
34	35	16.5884	15.2491
35	45	15.9411	15.647
36	55	17.0018	16.5699
37	65	17.3752	16.9114
38	75	16.9936	16.7714
39	85	16.8463	16.8399
40	95	17.0383	16.4564
41	105	16.4595	16.4402
42	115	16.535	16.3817
43	125	16.4125	16.5911
44	135	16.4793	15.9825
45	145	16.6256	16.8542
46	155	16.3114	16.709
47	165	16.039	16.0221
48	175	15.9572	15.6226
49	185	15.4841	15.7455
50	195	14.9995	14.9583

51	205	15.1169	14.1862
52	215	15.2321	14.3117
53	225	15.2535	13.695
54	235	15.0617	13.2541
55	245	14.9217	12.5911
56	255	14.348	12.5925
57	265	13.048	12.3824
58	275	12.2545	12.3342
59	285	11.6941	11.748
60	295	11.0258	10.9852
61	305	10.6543	10.0807
62	315	10.8738	9.5561
63	325	10.9338	9.3545
64	335	10.733	9.0021
65	345	10.5609	9.2453
66	355	10.4257	9.5446
67	365	10.7225	9.4662
68	375	10.9237	9.7891
69	385	10.9506	10.4914
70	395	11.2306	10.8319
71	405	11.0122	10.9832
72	415	11.162	11.2434
73	425	10.7833	11.1245
74	435	11.0825	11.0397
75	445	11.0875	10.894
76	455	11.4429	10.995
77	465	10.6452	10.9015
78	475	10.4559	10.6517
79	485	9.6027	9.8106
80	495	9.092	9.5418

Fig6BPSTH_monkeyH:

	Time_(ms)	Preferred	Anti-preferred
1	-295	11.5663	12.3877
2	-285	11.254	12.3001
3	-275	11.1641	12.3482
4	-265	10.9693	12.0029
5	-255	11.1881	12.2428
6	-245	11.1101	11.8269
7	-235	11.8576	12.1127
8	-225	12.3481	12.5379
9	-215	12.7106	13.0319
10	-205	12.809	12.7674
11	-195	12.9483	12.6902
12	-185	12.3791	12.9068
13	-175	12.3286	12.6447
14	-165	12.2716	12.5598
15	-155	11.6011	12.7197
16	-145	11.5187	12.857
17	-135	11.9878	12.2732
18	-125	11.7352	12.8369
19	-115	11.5802	13.0304
20	-105	11.9894	13.3671
21	-95	12.0602	13.1615
22	-85	11.4849	13.8033
23	-75	11.8249	13.4351
24	-65	11.8066	12.8096
25	-55	11.8017	12.8121
26	-45	12.8926	14.3469
27	-35	15.3671	16.0893
28	-25	16.8595	17.4929
29	-15	18.3013	19.1258
30	-5	19.8493	20.0658
31	5	19.1418	18.8956
32	15	17.0236	17.1792
33	25	16.171	16.3964
34	35	15.8519	16.1053
35	45	14.7788	15.2687
36	55	14.688	15.1351
37	65	14.4671	14.8162
38	75	13.5413	13.7681
39	85	12.3828	12.2365
40	95	12.0204	11.3035
41	105	11.4334	10.6246
42	115	11.3928	10.1325
43	125	11.6468	10.3029
44	135	11.8158	10.5685
45	145	11.6137	10.4079
46	155	11.8852	11.033
47	165	12.0954	11.5655
48	175	12.2988	11.8583
49	185	12.0254	12.0402
50	195	12.1551	12.7955
51	205	13.0049	13.3282
52	215	12.9797	13.1936
53	225	12.4456	13.1169
54	235	12.6527	12.7632
55	245	12.6754	12.0553
56	255	11.3851	11.0027
57	265	10.6852	10.4788
58	275	10.4991	9.8746
59	285	10.0252	9.9294
60	295	9.2609	9.4357
61	305	8.78	9.2558
62	315	8.6542	8.7052
63	325	8.5114	8.4833
64	335	8.2719	8.0042
65	345	8.2196	8.4123
66	355	8.769	8.1678
67	365	9.0587	8.7353
68	375	8.9361	9.3839
69	385	9.4108	9.8177
70	395	9.7387	10.0816
71	405	9.6731	10.8827
72	415	9.8723	10.8304
73	425	9.8973	10.475
74	435	9.522	10.7901
75	445	9.5642	10.8067
76	455	9.806	10.9858
77	465	9.6302	11.0404
78	475	9.3996	10.9811
79	485	8.9485	10.2635
80	495	8.491	9.4706

Fig6CPSTH_monkeyE:

	Time_(ms)	Preferred	Anti-preferred
1	-295	6.6643	6.6146
2	-285	6.8988	6.6112
3	-275	6.6082	6.3299
4	-265	6.7617	6.0975
5	-255	7.0314	5.9329
6	-245	7.2826	6.0413
7	-235	7.1008	5.9828
8	-225	7.5844	6.074

9	-215	7.6387	5.8088
10	-205	7.4634	5.6973
11	-195	7.3266	5.4195
12	-185	7.4496	5.3315
13	-175	7.2753	5.1273
14	-165	7.0902	5.4637
15	-155	7.6209	5.5855
16	-145	8.06	5.657
17	-135	7.7107	6.1589
18	-125	8.0609	6.3445
19	-115	8.3086	6.1937
20	-105	8.0064	6.3839
21	-95	7.5054	6.3191
22	-85	7.9702	6.1537
23	-75	7.6618	5.944
24	-65	7.3229	6.1357
25	-55	7.5006	5.8633
26	-45	7.339	5.7664
27	-35	6.9706	5.8804
28	-25	7.121	6.4077
29	-15	7.3895	6.453
30	-5	6.9433	6.5956
31	5	7.2255	7.1892
32	15	8.0699	7.5025
33	25	8.0875	7.9244
34	35	8.1852	8.6096
35	45	8.4253	9.3173
36	55	8.7357	10.0759
37	65	8.8467	10.8132
38	75	8.9727	11.4437
39	85	9.3911	11.5827
40	95	9.5218	11.6206
41	105	8.9588	10.3391
42	115	8.0015	9.2123
43	125	7.4719	7.9568
44	135	6.5863	7.216
45	145	5.9605	6.6486
46	155	6.0772	6.9159
47	165	6.4683	6.5154
48	175	6.4319	6.6233
49	185	6.9702	6.6884
50	195	7.8888	7.0692
51	205	8.2041	7.3927
52	215	8.5193	8.6205
53	225	9.2135	8.9033
54	235	9.2101	9.1364
55	245	9.3411	8.8504
56	255	9.6215	8.7682
57	265	9.6523	8.0169
58	275	9.3308	7.6784
59	285	9.0416	7.322
60	295	8.6492	7.4794
61	305	8.2751	7.5116
62	315	8.1024	8.0346
63	325	7.9146	7.8261
64	335	7.9377	8.0957
65	345	8.1548	7.9721
66	355	8.123	7.8011
67	365	7.6661	7.3671
68	375	7.8214	7.6644
69	385	8.1432	7.9759
70	395	7.958	8.2627
71	405	8.3248	8.6735
72	415	8.7118	9.2929
73	425	8.6207	9.9291
74	435	8.5544	9.7376
75	445	8.5101	9.5724
76	455	8.5129	9.2552
77	465	7.9738	8.6075
78	475	7.8974	7.6746
79	485	7.9896	7.1776
80	495	8.0382	7.2738

Fig6DPSTH_monkeyE:

	Time_(ms)	Preferred	Anti-preferred
1	-295	7.3263	6.0092
2	-285	7.1993	5.8581
3	-275	7.3221	5.9155
4	-265	7.2398	6.0509
5	-255	7.1808	6.0675
6	-245	6.8598	6.5494
7	-235	7.0029	6.6198
8	-225	7.2188	6.7418
9	-215	7.4029	6.3377
10	-205	7.3714	6.291
11	-195	7.4818	5.8766
12	-185	7.4089	5.9587
13	-175	7.328	6.0484
14	-165	6.989	6.3218
15	-155	7.0877	6.4714
16	-145	7.1333	6.5399
17	-135	6.9511	6.1158
18	-125	6.7011	5.9735
19	-115	7.0091	5.8028
20	-105	6.7226	5.8407
21	-95	6.5281	6.0232
22	-85	6.6912	6.3836
23	-75	6.8024	6.4182
24	-65	7.1838	6.4205
25	-55	7.5742	6.3737
26	-45	7.3254	5.9667
27	-35	7.2862	5.7165
28	-25	7.5089	6.0069
29	-15	7.0667	6.3652
30	-5	6.9439	6.3091
31	5	7.1251	7.0287
32	15	7.3156	8.2333
33	25	7.3356	8.5191
34	35	7.9797	8.6236
35	45	8.6282	9.1341
36	55	8.989	9.2094
37	65	9.257	9.3028
38	75	9.858	9.4337
39	85	10.0311	9.8038
40	95	9.5512	9.7956
41	105	9.1392	9.2534
42	115	8.3007	8.2236
43	125	7.5406	7.6825
44	135	6.3726	7.0336
45	145	6.0866	6.3635
46	155	5.8521	6.2003
47	165	6.0582	5.9775
48	175	5.7644	6.0738
49	185	6.1287	6.3201
50	195	6.3438	6.6735

51	205	6.8641	6.99
52	215	7.4355	7.7104
53	225	8.0424	7.7678
54	235	8.2941	7.9602
55	245	8.6153	8.3309
56	255	8.8686	8.5336
57	265	8.9405	8.5434
58	275	8.9151	8.4044
59	285	8.7116	8.0481
60	295	8.3872	7.9507
61	305	8.2758	7.4878
62	315	7.9481	7.2058
63	325	7.7684	7.6841
64	335	7.8779	8.1843
65	345	8.1954	8.0559
66	355	8.1697	8.3099
67	365	8.3353	8.3384
68	375	8.4553	7.5733
69	385	8.3713	7.6411
70	395	8.0566	8.0946
71	405	8.2075	8.5513
72	415	8.1664	9.2172
73	425	8.0728	9.9939
74	435	8.1691	10.0004
75	445	8.1906	9.6854
76	455	8.0378	9.4982
77	465	7.8285	8.6919
78	475	8.1996	8.6588
79	485	8.253	8.4706
80	495	8.3933	8.3221

Fig6EPSTH_monkeyH:

	Time_(ms)	Mean_difference	CI_of_difference
1	-295	-1.1913	2.0819
2	-285	-0.74486	1.6891
3	-275	-0.15261	1.5015
4	-265	-0.047027	1.4058
5	-255	0.71556	1.5962
6	-245	1.1622	1.5941
7	-235	0.88356	1.6027
8	-225	0.92277	1.5517
9	-215	0.31532	1.5492
10	-205	-0.47627	1.31
11	-195	-0.83398	1.3591
12	-185	-0.94246	1.5273
13	-175	-1.9597	1.6314
14	-165	-0.96963	1.5871
15	-155	-0.70902	1.5915
16	-145	-0.80982	1.4152
17	-135	-0.18382	1.3235
18	-125	0.79886	1.4354
19	-115	0.82917	1.6509
20	-105	0.74753	1.6812
21	-95	0.57221	1.736
22	-85	-0.36412	2.0907
23	-75	-0.91036	2.355
24	-65	-1.6249	2.5437
25	-55	-1.5757	2.6306
26	-45	-1.8418	2.4895
27	-35	-1.5295	1.8721
28	-25	-1.4474	1.7151
29	-15	-0.6443	1.4772
30	-5	-0.03844	1.3392
31	5	0.79246	1.0842
32	15	1.0071	1.3926
33	25	1.6275	1.3723
34	35	1.3393	1.3352
35	45	0.29402	1.5363
36	55	0.43194	1.6353
37	65	0.46376	1.4742
38	75	0.22224	1.3401
39	85	0.0064073	1.439
40	95	0.58193	1.2885
41	105	0.019306	1.4807
42	115	0.15331	1.6179
43	125	-0.17867	1.7002
44	135	0.49678	1.7945
45	145	-0.22865	1.6496
46	155	-0.39767	1.7536
47	165	0.016985	1.6604
48	175	0.33457	1.4282
49	185	-0.26144	1.5741
50	195	0.041268	1.6871
51	205	0.93068	1.7831
52	215	0.92041	1.8337
53	225	1.5584	1.5929
54	235	1.8075	1.5052
55	245	2.3307	1.5517
56	255	1.7555	1.7504
57	265	0.66566	1.8751
58	275	-0.079706	1.7855
59	285	-0.05392	1.4321
60	295	0.040596	1.2919
61	305	0.57357	1.2703
62	315	1.3177	1.4252
63	325	1.5793	1.4723
64	335	1.7309	1.6964
65	345	1.3155	1.6601
66	355	0.88105	1.8885
67	365	1.2563	1.728
68	375	1.1346	1.533
69	385	0.45918	1.5011
70	395	0.39869	1.4975
71	405	0.029005	1.3402
72	415	-0.081382	1.6057
73	425	-0.34119	1.3402
74	435	0.042809	1.2172
75	445	0.1935	1.2728
76	455	0.44786	1.2826
77	465	-0.25635	1.4849
78	475	-0.19581	1.4618
79	485	-0.20789	1.4992
80	495	-0.44982	1.3567

Fig6FPSTH_monkeyH:

	Time_(ms)	Mean_difference	CI_of_difference
1	-295	-0.82143	1.5739
2	-285	-1.0461	1.626
3	-275	-1.1841	1.8388
4	-265	-1.0336	1.7483
5	-255	-1.0547	1.4687

6	-245	-0.71677	1.6205
7	-235	-0.25511	1.719
8	-225	-0.18973	1.7852
9	-215	-0.32125	1.7812
10	-205	0.041609	1.92
11	-195	0.25805	1.9573
12	-185	-0.52772	1.8235
13	-175	-0.3161	2.1455
14	-165	-0.28816	1.999
15	-155	-1.1186	2.092
16	-145	-1.3383	2.3765
17	-135	-0.28538	2.2644
18	-125	-1.1016	2.7065
19	-115	-1.4503	2.7586
20	-105	-1.3777	2.7412
21	-95	-1.1013	1.9694
22	-85	-2.3183	1.8975
23	-75	-1.6102	1.7368
24	-65	-1.003	1.4691
25	-55	-1.0104	1.545
26	-45	-1.4543	1.7344
27	-35	-0.72228	1.6397
28	-25	-0.63339	1.3791
29	-15	-0.82448	1.0342
30	-5	-0.21653	1.0012
31	5	0.24621	1.7168
32	15	-0.15563	1.8732
33	25	-0.22544	1.5742
34	35	-0.25336	1.608
35	45	-0.4899	1.2068
36	55	-0.44703	0.94826
37	65	-0.34906	0.84669
38	75	-0.22685	0.85431
39	85	0.1463	1.0161
40	95	0.71689	1.2357
41	105	0.8088	1.3559
42	115	1.2603	1.4736
43	125	1.3439	1.7318
44	135	1.2473	1.7642
45	145	1.2058	1.69
46	155	0.85215	1.448
47	165	0.52995	1.3687
48	175	0.44047	1.5033
49	185	-0.014807	1.3875
50	195	-0.64036	1.4956
51	205	-0.32336	1.3009
52	215	-0.21384	1.3636
53	225	-0.67128	1.3232
54	235	-0.11054	1.0772
55	245	0.6201	1.4822
56	255	0.38245	1.8129
57	265	0.20632	1.7835
58	275	0.62444	1.726
59	285	0.095831	1.851
60	295	-0.17478	1.4951
61	305	-0.47578	1.3597
62	315	-0.051024	1.5439
63	325	0.028066	1.5328
64	335	0.26775	1.4487
65	345	-0.19264	1.6687
66	355	0.60118	1.9656
67	365	0.32341	1.9011
68	375	-0.44776	1.7966
69	385	-0.40691	1.692
70	395	-0.34288	1.1756
71	405	-1.2097	1.3038
72	415	-0.95809	1.306
73	425	-0.57768	1.7342
74	435	-1.2682	1.8474
75	445	-1.2425	1.6815
76	455	-1.1797	1.5221
77	465	-1.4102	1.4435
78	475	-1.5815	1.6584
79	485	-1.315	1.4764
80	495	-0.97963	1.3297

Fig6GPSTH_monkeyE:

	Time_(ms)	Mean_difference	CI_of_difference
1	-295	0.049706	1.2363
2	-285	0.28762	1.2486
3	-275	0.27833	1.1219
4	-265	0.66422	1.1084
5	-255	1.0984	1.1166
6	-245	1.2413	1.2024
7	-235	1.118	1.2154
8	-225	1.5104	1.1523
9	-215	1.8298	1.3464
10	-205	1.7661	1.2508
11	-195	1.9071	1.3287
12	-185	2.1181	1.3613
13	-175	2.148	1.2706
14	-165	1.6264	1.2995
15	-155	2.0354	1.5476
16	-145	2.403	1.6117
17	-135	1.5517	1.1675
18	-125	1.7164	1.1355
19	-115	2.1149	1.3407
20	-105	1.6225	1.1891
21	-95	1.1863	1.3267
22	-85	1.8164	1.2614
23	-75	1.7178	1.4113
24	-65	1.1872	1.2645
25	-55	1.6373	1.5288
26	-45	1.5727	1.4669
27	-35	1.0902	1.4668
28	-25	0.71336	1.3195
29	-15	0.93648	1.4615
30	-5	0.34763	1.2495
31	5	0.036328	1.1483
32	15	0.56736	0.9814
33	25	0.16306	0.9913
34	35	-0.42441	1.0802
35	45	-0.89197	1.052
36	55	-1.3402	1.4245
37	65	-1.9665	1.4392
38	75	-2.471	1.538
39	85	-2.1917	1.5244
40	95	-2.0988	1.372
41	105	-1.3803	1.2341
42	115	-1.2108	1.1972
43	125	-0.4849	1.1398
44	135	-0.62971	1.5476
45	145	-0.6881	1.5188
46	155	-0.83873	1.5019

47	165	-0.04713	1.4841
48	175	-0.19137	1.2127
49	185	0.28178	1.2928
50	195	0.81952	1.1798
51	205	0.81139	1.2985
52	215	-0.1012	1.467
53	225	0.31023	1.5437
54	235	0.073632	1.6404
55	245	0.49063	1.5989
56	255	0.85332	1.4903
57	265	1.6354	1.4404
58	275	1.6524	1.3701
59	285	1.7196	1.2229
60	295	1.1697	1.4193
61	305	0.76354	1.4041
62	315	0.06782	1.5203
63	325	0.088547	1.3976
64	335	-0.15798	1.5121
65	345	0.18271	1.4071
66	355	0.32186	1.4976
67	365	0.29896	1.4213
68	375	0.15699	1.4675
69	385	0.16733	1.3509
70	395	-0.30471	1.3449
71	405	-0.34866	1.6107
72	415	-0.58114	1.5905
73	425	-1.3084	1.6999
74	435	-1.1832	1.5237
75	445	-1.0623	1.2557
76	455	-0.74233	1.0024
77	465	-0.63371	1.0958
78	475	0.22273	1.2199
79	485	0.81206	1.4014
80	495	0.76435	1.3316

Fig6HPSTH_monkeyE:

	Time_(ms)	Mean_difference	CI_of_difference
1	-295	1.3171	1.1571
2	-285	1.3411	1.1175
3	-275	1.4066	1.0946
4	-265	1.1889	1.0029
5	-255	1.1133	1.2042
6	-245	0.31041	1.1511
7	-235	0.38315	1.2283
8	-225	0.47697	0.98795
9	-215	1.0652	1.0052
10	-205	1.0805	0.9794
11	-195	1.6052	1.0829
12	-185	1.4502	1.1536
13	-175	1.2796	1.1972
14	-165	0.6672	1.1713
15	-155	0.61634	1.155
16	-145	0.59344	1.1493
17	-135	0.83523	0.96163
18	-125	0.72759	1.1239
19	-115	1.2063	1.4272
20	-105	0.88187	1.3082
21	-95	0.50486	1.5757
22	-85	0.30762	1.5076
23	-75	0.38412	1.4283
24	-65	0.76326	1.3824
25	-55	1.2005	1.4944
26	-45	1.3587	1.6424
27	-35	1.5697	1.7707
28	-25	1.5021	1.5458
29	-15	0.70152	1.5315
30	-5	0.6348	1.4645
31	5	0.096418	1.3479
32	15	-0.91771	1.5312
33	25	-1.1835	1.638
34	35	-0.64397	1.4427
35	45	-0.50592	1.28
36	55	-0.2204	1.4263
37	65	-0.045706	1.5443
38	75	0.42431	1.6978
39	85	0.22737	1.6632
40	95	-0.24435	1.4911
41	105	-0.11421	1.5859
42	115	0.077109	1.6084
43	125	-0.14188	1.552
44	135	-0.66104	1.1139
45	145	-0.27699	1.0982
46	155	-0.34819	1.0996
47	165	0.080735	1.2047
48	175	-0.30945	1.2427
49	185	-0.19134	1.0993
50	195	-0.32975	1.076
51	205	-0.12589	1.1627
52	215	-0.27486	1.2006
53	225	0.27464	1.2421
54	235	0.33393	1.8051
55	245	0.28446	1.7929
56	255	0.33501	1.6519
57	265	0.39703	1.5994
58	275	0.51068	1.476
59	285	0.66342	1.2678
60	295	0.43651	1.1688
61	305	0.78801	1.485
62	315	0.74225	1.4469
63	325	0.084311	1.2626
64	335	-0.30636	1.3852
65	345	0.13952	1.8182
66	355	-0.14019	1.5876
67	365	-0.0031619	1.3511
68	375	0.88206	1.1899
69	385	0.73018	1.1517
70	395	-0.037977	1.1008
71	405	-0.34383	1.3039
72	415	-1.0508	1.5609
73	425	-1.9211	1.6116
74	435	-1.8313	1.7256
75	445	-1.4947	1.6818
76	455	-1.4604	1.8487
77	465	-0.86338	1.6711
78	475	-0.45918	1.4149
79	485	-0.21754	1.271
80	495	0.071217	1.3048

S6 Data. The data presented in S1 Fig.

Note:
FigS1PSTH_monkeyH.txt contains the values for the population average PSTHs for monkey H in Figure S1
FigS1PSTH_monkeyE.txt contains the values for the population average PSTHs for monkey E in Figure S1

FigS1PSTH_monkeyH:

	Time_(ms)	Mean_sensory_response	SEM_sensory_response	Mean_remapped_response	SEM_remapped_response
1	-295	0.018483	0.0087484	0.10822	0.072263
2	-285	0.0075147	0.0090643	0.057926	0.06414
3	-275	0.0050541	0.0085317	0.065446	0.064627
4	-265	-0.0028804	0.0090926	0.0098769	0.062388
5	-255	-0.0060576	0.010667	-0.026778	0.053476
6	-245	-0.012807	0.010842	0.015623	0.066477
7	-235	-0.0083755	0.0091578	0.04118	0.076049
8	-225	-0.011824	0.0099829	0.0047123	0.069882
9	-215	-0.0087666	0.008309	0.023912	0.061616
10	-205	-0.0095901	0.0090808	0.048778	0.063378
11	-195	-0.013404	0.010736	0.0012119	0.066929
12	-185	-0.0051188	0.011764	-0.051512	0.077712
13	-175	-0.00051309	0.012575	-0.030814	0.091626
14	-165	-0.0050449	0.011759	-0.11122	0.083358
15	-155	-0.0097405	0.010591	-0.16951	0.085243
16	-145	-0.00041036	0.010465	-0.12079	0.080888
17	-135	-0.0081347	0.0098606	-0.076397	0.083383
18	-125	-0.0050513	0.013589	-0.094657	0.10419
19	-115	-0.0031991	0.012108	-0.058781	0.10079
20	-105	-0.0085734	0.012993	-0.1115	0.10384
21	-95	-0.0012513	0.013528	-0.043681	0.11291
22	-85	0.0058914	0.016683	-0.0035871	0.10499
23	-75	0.0018651	0.016441	0.020861	0.10184
24	-65	-0.00024995	0.01691	0.048439	0.086472
25	-55	0.014806	0.017032	0.2013	0.094872
26	-45	0.014026	0.01521	0.16849	0.10024
27	-35	0.0083577	0.012537	0.085137	0.088044
28	-25	0.013476	0.0096147	0.044095	0.089774
29	-15	0.021143	0.0134	0.046255	0.098309
30	-5	0.010375	0.011478	-0.092232	0.09289
31	5	0.052522	0.018569	-0.10793	0.10285
32	15	0.18534	0.041391	0.032845	0.099684
33	25	0.35889	0.059491	0.15078	0.11409
34	35	0.5141	0.070269	0.19397	0.12614
35	45	0.69684	0.078485	0.33438	0.14372
36	55	0.83927	0.083345	0.49333	0.19983
37	65	0.90235	0.083165	0.5135	0.20227
38	75	0.94303	0.085768	0.6232	0.22274
39	85	0.99791	0.093135	0.80001	0.24323
40	95	1.0031	0.096868	0.89191	0.25078
41	105	0.99645	0.096199	0.9633	0.25025
42	115	0.97456	0.094252	1.0265	0.24553
43	125	0.92663	0.090222	1.0124	0.23023
44	135	0.86893	0.085549	0.91089	0.20635
45	145	0.83548	0.083552	0.8947	0.20642
46	155	0.80159	0.080654	0.71295	0.19675
47	165	0.77343	0.077761	0.55538	0.17328
48	175	0.74514	0.074534	0.45657	0.16867
49	185	0.71274	0.071131	0.36548	0.14387
50	195	0.68394	0.068797	0.27501	0.12492
51	205	0.66135	0.069996	0.25509	0.12674

52	215	0.65593	0.069695	0.32982	0.1115
53	225	0.64393	0.068822	0.30676	0.12063
54	235	0.64353	0.067952	0.36831	0.10197
55	245	0.66145	0.068281	0.38609	0.10029
56	255	0.67317	0.066136	0.48482	0.11705
57	265	0.66316	0.064342	0.44795	0.12302
58	275	0.68471	0.066538	0.50496	0.1563
59	285	0.69092	0.068363	0.52067	0.17338
60	295	0.6916	0.06791	0.47896	0.18086
61	305	0.68185	0.067732	0.37493	0.15343
62	315	0.67624	0.066812	0.3238	0.12536
63	325	0.65989	0.065315	0.24765	0.11748
64	335	0.65519	0.064465	0.15065	0.10423
65	345	0.65317	0.065278	0.098227	0.08998
66	355	0.64843	0.063348	0.041072	0.096331
67	365	0.64817	0.064423	0.0059498	0.10999
68	375	0.64955	0.063965	0.033064	0.099511
69	385	0.6509	0.065023	0.050893	0.10366
70	395	0.6353	0.062316	0.070514	0.10261
71	405	0.61958	0.060366	0.039878	0.092901
72	415	0.61185	0.058786	0.074315	0.082662
73	425	0.59564	0.056829	0.044805	0.091804
74	435	0.59533	0.05575	0.064729	0.081799
75	445	0.60091	0.056319	0.11625	0.093831
76	455	0.61977	0.056768	0.23996	0.082316
77	465	0.62337	0.056353	0.23737	0.079022
78	475	0.62812	0.057333	0.23624	0.070102
79	485	0.62523	0.057231	0.16445	0.043497
80	495	0.61608	0.057994	0.11116	0.053274

FigS1PSTH_monkeyE:

	Time_(ms)	Mean_sensory_response	SEM_sensory_response	Mean_remapped_response	SEM_remapped_response
1	-295	-0.0062942	0.012258	0.19539	0.23923
2	-285	-0.0063491	0.011375	0.20837	0.22901
3	-275	-0.0027549	0.011101	0.0913	0.23306
4	-265	-0.00022307	0.010557	0.089795	0.22772
5	-255	-0.0041986	0.010758	-0.10005	0.21688
6	-245	-0.0046777	0.0094813	-0.022359	0.22324
7	-235	-0.0046842	0.0098708	-0.13587	0.22414
8	-225	-0.010737	0.01222	-0.30034	0.30493
9	-215	-0.0072903	0.010751	-0.3657	0.2815
10	-205	0.0029717	0.011351	-0.21887	0.26833
11	-195	0.0067067	0.0096024	-0.33954	0.28521
12	-185	0.0088678	0.010257	-0.23041	0.28349
13	-175	0.015081	0.0086137	-0.022313	0.21181
14	-165	0.01836	0.009293	0.066552	0.21507
15	-155	0.014006	0.0081962	0.1924	0.2634
16	-145	0.0076278	0.0099851	0.3	0.30503
17	-135	0.0047657	0.0094554	0.26634	0.24683
18	-125	-0.0011722	0.0092663	0.24408	0.24212
19	-115	-0.010218	0.0088895	0.17961	0.21416
20	-105	-0.0071747	0.0094816	0.15861	0.2138
21	-95	-0.0026789	0.0096664	0.072437	0.22523
22	-85	-0.0016281	0.011736	0.13953	0.21879
23	-75	5.1622e-05	0.01483	0.00095034	0.25546
24	-65	-0.0038675	0.015453	-0.086454	0.24237
25	-55	-0.0062266	0.012916	-0.22783	0.19438
26	-45	0.00032782	0.012479	-0.13174	0.19402
27	-35	-0.0080286	0.0098145	-0.15397	0.22652
28	-25	-0.0047772	0.0096986	-0.014821	0.22211

29	-15	0.0028886	0.012432	0.085615	0.27287
30	-5	0.011325	0.0148	0.059305	0.24531
31	5	0.073296	0.024313	0.21045	0.25776
32	15	0.22874	0.035417	0.1996	0.21862
33	25	0.4259	0.051491	0.12434	0.21302
34	35	0.65032	0.068949	0.12816	0.21694
35	45	0.84363	0.085614	0.17563	0.24202
36	55	0.97251	0.094725	0.27191	0.25214
37	65	0.98825	0.096767	0.55958	0.29421
38	75	0.92801	0.090911	0.69781	0.30155
39	85	0.83392	0.091083	0.75678	0.30194
40	95	0.75599	0.088526	0.93394	0.34351
41	105	0.68859	0.08321	0.60722	0.32607
42	115	0.64771	0.079383	0.36991	0.31986
43	125	0.63243	0.074325	0.22961	0.26404
44	135	0.62917	0.070373	0.17081	0.20612
45	145	0.62349	0.066234	0.14461	0.20871
46	155	0.62238	0.065265	0.23985	0.25471
47	165	0.62862	0.067664	0.21906	0.2041
48	175	0.62934	0.068192	0.35227	0.21037
49	185	0.62433	0.067762	0.5158	0.2373
50	195	0.62239	0.068172	0.56405	0.25231
51	205	0.60109	0.069212	0.58294	0.28753
52	215	0.57602	0.064043	0.87504	0.30961
53	225	0.56892	0.063615	0.91175	0.34862
54	235	0.54051	0.058165	0.76062	0.3962
55	245	0.5264	0.058327	0.72832	0.41611
56	255	0.52244	0.054895	0.93194	0.44834
57	265	0.5238	0.05449	0.72243	0.3846
58	275	0.51284	0.05305	0.58923	0.34188
59	285	0.52235	0.054618	0.55248	0.28383
60	295	0.52513	0.053787	0.47665	0.28428
61	305	0.54252	0.059891	0.39245	0.30651
62	315	0.52833	0.058073	0.32065	0.26403
63	325	0.52646	0.060293	0.26349	0.26242
64	335	0.51418	0.057107	0.19495	0.31293
65	345	0.5019	0.059131	0.19367	0.31006
66	355	0.4817	0.056403	-0.13986	0.25456
67	365	0.49184	0.05857	-0.26604	0.23646
68	375	0.48162	0.05596	-0.13604	0.25717
69	385	0.48441	0.058584	0.118	0.21237
70	395	0.48331	0.055877	0.11072	0.18126
71	405	0.47328	0.052872	0.2847	0.22181
72	415	0.46114	0.053132	0.49842	0.23663
73	425	0.46716	0.054852	0.46395	0.29863
74	435	0.4644	0.053609	0.37135	0.27079
75	445	0.45077	0.053822	0.17287	0.22165
76	455	0.4492	0.055065	0.26648	0.20773
77	465	0.44914	0.05482	0.15332	0.24302
78	475	0.43461	0.053617	0.070683	0.25635
79	485	0.43768	0.056573	0.063862	0.23943
80	495	0.44366	0.053398	0.24806	0.27574

S7 Data. The data presented in S2 Fig.

Note:
FigS2PSTH_monkeyH.txt contains the values for the population average PSTHs for monkey H in Figure S2
FigS2PSTH_monkeyE.txt contains the values for the population average PSTHs for monkey E in Figure S2

FigS2PSTH_monkeyH:

	Time_(ms)	Mean_attentional_effect	CI
1	-295	0.58137	2.0834
2	-285	-0.2098	1.7531
3	-275	0.18278	1.7038
4	-265	-0.29116	1.672
5	-255	-0.45375	1.7414
6	-245	0.6861	1.9764
7	-235	1.159	1.8704
8	-225	-0.095437	1.8282
9	-215	-0.48814	1.9327
10	-205	-0.56252	1.7543
11	-195	-0.82488	1.9822
12	-185	-0.43742	2.0904
13	-175	0.16235	2.2372
14	-165	1.323	2.2254
15	-155	0.85268	2.6838
16	-145	1.3076	3.1539
17	-135	0.83204	2.7651
18	-125	-0.21677	2.6267
19	-115	0.43878	2.3346
20	-105	1.4352	2.1746
21	-95	1.2287	1.822
22	-85	1.2752	1.7942
23	-75	2.0771	1.9267
24	-65	1.0409	1.8677
25	-55	0.78477	2.2878
26	-45	1.2194	2.3602
27	-35	-0.23966	2.4653
28	-25	-0.48147	2.0871
29	-15	0.089871	2.0876
30	-5	-0.050494	2.3212
31	5	-1.4054	2.6254
32	15	0.84223	2.858
33	25	2.9415	2.978
34	35	3.5813	2.8867
35	45	4.6816	3.2726
36	55	5.1565	3.2593
37	65	5.4373	4.1226
38	75	3.1391	3.9811
39	85	2.3683	3.9057
40	95	0.99861	4.0923
41	105	4.5326	3.8466
42	115	2.8794	4.2088
43	125	4.4266	3.8296
44	135	4.9388	4.3853
45	145	6.4934	4.1592
46	155	4.2852	4.3129
47	165	7.4011	4.1065
48	175	8.0754	4.2127
49	185	8.0269	3.8024
50	195	8.6791	3.8534
51	205	9.9012	4.73
52	215	8.4512	4.4731
53	225	7.4847	4.3772
54	235	7.2583	4.2555
55	245	5.4898	4.0783
56	255	4.4779	4.2193
57	265	2.678	3.5071
58	275	2.7371	3.5878
59	285	2.1842	4.128
60	295	2.0902	3.8349
61	305	1.7857	3.7985
62	315	2.8525	3.7617
63	325	3.614	3.8046
64	335	5.1329	3.918
65	345	6.9315	4.021
66	355	8.0287	4.0042
67	365	9.5929	4.0122
68	375	10.3884	4.6736
69	385	11.5895	4.4531
70	395	11.9875	4.4723
71	405	12.4644	4.1003
72	415	12.8581	4.3197
73	425	11.7018	4.399
74	435	11.0352	4.5748
75	445	10.9372	4.8373
76	455	10.3114	4.895
77	465	9.8787	4.4818
78	475	9.1411	4.4496
79	485	8.667	4.2825
80	495	8.2812	4.3975

FigS2PSTH_monkeyE:

	Time_(ms)	Mean_attentional_effect	CI
1	-295	0.87367	1.4899
2	-285	0.879	1.4558
3	-275	0.26427	1.7511
4	-265	0.24599	1.7091
5	-255	0.039469	1.6269
6	-245	-0.47551	1.7079
7	-235	-0.82249	1.6776
8	-225	-0.83786	1.5989
9	-215	-1.0577	1.8025
10	-205	-0.9445	1.6527
11	-195	-0.69962	1.438
12	-185	0.10182	1.3538
13	-175	0.23558	1.5079
14	-165	0.21188	1.3539
15	-155	-0.58115	1.2568
16	-145	0.63103	1.5457
17	-135	0.35163	1.5634
18	-125	0.27468	1.5281
19	-115	0.25633	1.6703
20	-105	0.94704	1.889
21	-95	-0.26838	1.8503
22	-85	-0.3316	1.7863
23	-75	-0.73648	1.9131
24	-65	-0.68576	1.3362
25	-55	-1.2533	1.7189
26	-45	-0.51178	1.7934
27	-35	-0.58727	1.657
28	-25	-0.065759	1.9832
29	-15	0.47966	2.2304
30	-5	1.3192	2.0301
31	5	1.139	2.68
32	15	-0.26131	3.0205
33	25	-0.32825	3.2324
34	35	-2.834	3.5804
35	45	-2.156	3.6898
36	55	-1.935	3.9241
37	65	-0.66879	3.6644

38	75	1.2557	3.2863
39	85	3.8835	3.5045
40	95	3.9376	3.489
41	105	5.6002	2.8703
42	115	7.9642	2.473
43	125	8.1909	3.1376
44	135	9.3435	3.4418
45	145	10.3776	4.1636
46	155	7.9946	3.6993
47	165	5.8416	3.9476
48	175	6.4685	3.6792
49	185	5.2322	3.6579
50	195	3.5225	3.3327
51	205	5.6484	3.6555
52	215	8.4299	3.8193
53	225	6.7573	4.0693
54	235	8.6368	3.931
55	245	9.1342	3.9831
56	255	7.3508	4.4167
57	265	6.8344	4.8109
58	275	6.9894	5.5497
59	285	4.8494	5.1383
60	295	4.3564	5.1865
61	305	5.6535	4.8102
62	315	4.6821	3.9457
63	325	4.2472	4.2154
64	335	5.5825	3.9402
65	345	6.6659	3.6192
66	355	7.3216	4.0849
67	365	7.0167	4.2446
68	375	8.2359	4.3935
69	385	8.6967	3.7828
70	395	7.5067	3.563
71	405	6.3975	3.3548
72	415	7.6455	3.4001
73	425	7.0548	3.8473
74	435	5.8643	4.2205
75	445	7.784	4.4458
76	455	8.6023	4.5583
77	465	6.9934	4.7635
78	475	6.5831	4.2317
79	485	6.8496	3.9354
80	495	3.3792	3.5464

Additional supplementary materials 4: Example epars & mpars

Note: The epars define the time sequence of the experiment, the location of the stimulus, i.e. when and where to show the stimulus on the screen. The epars also on-line control the data collection and some events related to subject performance (such as eye position, time window of reaction etc.). The mpars controls the properties of the stimuli, such as the motion direction, speed, dot density, color of the RDP.

Example epars:

```
projectLeader tao
expCode trAttC

displayWindowOnSecondMonitor 0 0 200 200

trialProtocol 1 9
0 0 0 0 1 0
55    0 -320 -380    1    1
10   20 -320 -380    1    1
1 0 0 0 0 0
55    0 -320  380    1    1
10   20 -320  380    1    1
105 0 0 0 1 1
55   59 -320 -380    1    1
55   59 -320  380    1    1

displayCenter 0          1     0.29167        0.5
displayCenter 1    1  800    0

filenames&pathname 35 :trace:traceMpars:
Luminance.mpar
fixStim1.mpar
fixStim2.mpar
Cue.mpar
TP.mpar
T45.mpar
T90.mpar
T135.mpar
T180.mpar
T225.mpar
T270.mpar
T315.mpar
DP.mpar
D45.mpar
D90.mpar
D135.mpar
D180.mpar
D225.mpar
D270.mpar
D315.mpar
AttTP.mpar
AttDP.mpar
DPshort.mpar
fixStimlong.mpar
DPOff.mpar
AttTPF.mpar
AttDPF.mpar
D180Off.mpar
fixStim4.mpar
fixStim5.mpar
fixStim6.mpar
AttTP180.mpar
AttDP180.mpar
AttTPF180.mpar
AttDPF180.mpar

# class 5 and 6 fixation task (+60 frame to
+120frame, +~800ms to 1600ms)
# class 1 and 2 phase change after 1st FP
disappears ( +20 to +100 frames, ~+267ms to
+1333ms after 1st FP disappears)
# class 3 and 4 are prefered directions, cue in
cue out
# class 7 and 8 are antiprefered directions,
cue in cue out
# class 9-12 antipreference directions,
before(11-12) and after saccade(9-10).

classes 19
1 0 0 0 1 0 0 0 0 0 0 0 0
1 29 21 4 0 22 0 31 0 0 1 0 0
1 29 22 0 0 21 4 31 0 0 2 0 0
1 2 0 4 0 0 0 3 25 25 3 0 0
1 2 0 0 0 0 4 3 25 25 4 0 0
1 30 26 4 0 27 0 0 0 0 5 0 0
1 30 27 0 0 26 4 0 0 0 6 0 0
1 2 0 4 0 0 0 3 28 28 7 0 0
1 2 0 0 0 0 4 3 28 28 8 0 0

1 29 32 4 0 33 0 31 0 0 9 0 0
1 29 33 0 0 32 4 31 0 0 10 0 0
1 30 34 4 0 35 0 0 0 0 11 0 0
1 30 35 0 0 34 4 0 0 0 12 0 0
1 2 0 4 0 0 0 3 25 25 13 0 0
1 2 0 0 0 0 4 3 25 25 14 0 0
1 2 0 4 0 0 0 3 28 28 15 0 0
1 2 0 0 0 0 4 3 28 28 16 0 0
1 2 0 0 0 0 0 3 0 0 17 0 0
1 2 0 0 0 0 0 3 0 0 18 0 0

classFrequencyOption 0
```

```
# default is zero, this equates the number of
trials
waitForLever 10000
rewardDuration 90
leverDownRewardDuration 0
preLeverBeepDelay 2000
anticipatedResponseDuration 150
responseTimeWindow 600
#changed above from 500
hitDelay 1500
missDelay 1000
leverReleaseDuration 600
juicePin 1
fixpointIndexColor 255
backgroundIndexColor 200
fixPointSize 12
keyboardResponse FALSE
earlyResponsePermitted FALSE
fixPointVisibleBetweenTrials false
fixationRequired FALSE
collectEyePositions TRUE
fixAreaRadiusOfClass 0 80
preLeverFixRelaxation 2
smoothEyePositions 4
spikeSource 1
sampleSource 1
collectSpikes TRUE
numberOfTrials 9000
dotPosToBuffer FALSE
spikeRecSystem 3
eyePosDecay -20
provideWords TRUE
openDataFile
savePupilDiameter TRUE
```

Example mpars

fixStim1.mpar:

```
numberOfSurfaces 1 40 0
pixelradius      20
numberOfFrames 105
#qtRGBForeColor          6553 6553 0
qtIndexForeColor 255
qtSquare         -6      -6      6       6
```

fixStim2.mpar

```
numberOfSurfaces 1 40 0
pixelradius      10
numberOfFrames 105
#qtRGBForeColor          6553 6553 0
qtIndexForeColor 255
qtSquare         -6      -6      6       6
qtSuspendFix     105 125
qtFixFactor              105 -1   1.5
qtFixDispCtr     105 -1   1
```

fixStim6.mpar

```
numberOfSurfaces 1 40 0
pixelradius      10
numberOfFrames 300
#qtRGBForeColor          6553 6553 0
qtIndexForeColor 200
qtSquare         -6      -6      6       6
qtSuspendFix     105 125
qtFixFactor              105 -1   1.5
qtFixDispCtr     105 -1   1
```

DPOff.mpar

```
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 100
numberOfFrames 59
speed 8
shape circle
colorIndex 255
direction 240
```

AttTPF.mpar

```
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 100
numberOfFrames 150
speed 8
shape circle
colorIndex 255
direction 240
changePhase -60 140
directionTable 2 150  330
changePhase 10 10
direction 240
```

AttTP.mpar

```
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 100
numberOfFrames 250
speed 8
shape circle
colorIndex 255
direction 240
changePhase -125 205
directionTable 2 150  330
changePhase 10 10
direction 240
```

AttDP.mpar

```
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 100
numberOfFrames 250
```

speed 8
shape circle
colorIndex 255
direction 240
changePhase 125 205
directionTable 2 150 330
changePhase 10 10
direction 240

Cue.mpar
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 80
numberOfFrames 20
speed 0
shape circle
colorIndex 255

D180Off.mpar
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 100
numberOfFrames 59
speed 8
shape circle
colorIndex 255
direction 60

AttDP180.mpar
numberOfSurfaces 1 40 10
dotSize 4
pixelradius 100
numberOfFrames 250
speed 8
shape circle
colorIndex 255
direction 60
changePhase 125 205
directionTable 2 330 150
changePhase 10 10
direction 60

Chapter 5

General discussion

Humans and monkeys make two to three saccades per second on average when they are awake (Snodderly, 1987), and they are able to keep track of relevant visual stimuli while making saccadic eye-movements to scan a visual scene . Since the visual system mostly operates using retinotopic representations (Wurtz, 2008; Cavanagh, Hunt, Afraz et al., 2010; Marino and Mazer, 2016), in each visual area, a relevant visual stimulus (the target) at a fixed spatial location is represented by one neuronal population before the saccade and a different neuronal population after the saccade: we refer to these as the pre-saccadic target population and the post-saccadic target population respectively. As a result, to maximally and selectively enhance target processing (but not distractor processing) both before and after the saccade, a rapid, saccade-synchronized remapping of top-down attentional modulation from the pre-saccadic to the post-saccadic target population is optimal. Attentional enhancement would ideally be expected to be dominant at the pre-saccadic target population until just before saccade offset, and decay at or soon after saccade offset. Similarly, attentional enhancement would be expected to emerge at the post-saccadic target population at or soon after saccade offset. However, the time-course of the shift of top-down attention from the pre-saccadic to the post-saccadic target population across a saccade has never been explicitly measured.

We recorded the extracellular activity of single neurons in area MT of two macaque monkeys during a task that required them to make a saccade while maintaining attention on one of four moving random dot patterns (RDPs). In the first experiment, the attended stimulus was either in the neurons' pre-saccadic receptive field (RF) or directly opposite to it, while in the second experiment, the attended stimulus was either in the post-saccadic RF or directly opposite to it. By looking at the neuronal responses just before and after the eye movement, we were able to investigate the time course of the neuronal activity when the target was brought into or moved out of the neuron's RF by the saccade. Therefore, we investigated how attention modulation emerged and decayed in the neuronal activity in area MT across saccades by this experimental manipulation. We found, for the first time, that trans-saccadic attentional shift is well-synchronized to the saccade: attentional enhancement crosses over from the pre-saccadic to the post-saccadic target population at 31 and 52 ms after saccade offset in the two monkeys in area MT. Specifically, the results of our first experiment indicated that attentional enhancement of the pre-saccadic target population lingered after the saccade and disappeared by 50 ms after saccade offset in one monkey and by 100 ms in the other; and the results of our second experiment suggest

attentional enhancement of the post-saccadic target population emerged at saccade offset and within 50 ms of saccade offset in the two monkeys. We did not find any evidence for attentional enhancement of the post-saccadic target population before the saccade, even though our experimental design ensured that there would be a distractor-driven response before the saccade on which an attentional effect could be seen, if present.

By using a similar paradigm with finer temporal resolution, we also showed that the top-down spatial attention is fully available at the task-relevant location within 30 milliseconds after the saccade in human subjects. Given an onset latency of approximately 30 ms in MT (Bair, Cavanaugh, Smith et al., 2002), a visual change occurring 30 ms after saccade offset would reach MT by 60 ms after saccade offset, by which time attention would have crossed-over to the post-saccadic target population (as we show here). Further, our data indicated that under our task conditions, subjects very rarely confused a distractor stimulus for the target. Spatial attention and saccadic execution thus appeared to co-ordinate well to ensure that relevant objects were attentionally enhanced soon after the beginning of each eye fixation. Additionally, we did not find any evidence for a predictive, pre-saccadic shift of attention to the post-saccadic target population when the human subjects were doing the task. This is consistent with the fact that we and others (*cite Ong and Bisley)* have not found evidence for "predictive" pre-saccadic attentional remapping to the post-saccadic target population. The absence of predictive remapping in MT is particularly interesting, because a large body of previous work indicates that neurons in the lateral intraparietal area (LIP), frontal eye field (FEF), superior colliculus (SC), medial superior temporal area (MST) and in the ventral stream (areas V3a, V3 and V2) respond peri-saccadically as long as a visual stimulus could be anticipated in their receptive fields (RFs) after the saccade (Duhamel, Colby and Goldberg, 1992; Walker, Fitzgibbon and Goldberg, 1995; Umeno and Goldberg, 1997, 2001; Nakamura and Colby, 2002; Wurtz, Joiner and Berman, 2011; Inaba and Kawano, 2014). This "remapped response" is not a simple visual afferent response, because it appears even when the visual stimulus disappears just before the saccade (that would bring the stimulus location into the RF), so that no stimulus ever appears in the neurons' visual RF before or after the saccade. Further, in some neurons, it begins with a latency shorter than the normal visual latency and can even begin before saccade onset, in which case it has been referred to as "predictive remapping" (Duhamel, Colby and Goldberg, 1992). More commonly, the remapped response occurs post-saccadically, and when this occurs in a situation where there is no

post-saccadic stimulus in the RF because it disappeared before the saccade, the remapped response is referred to as a "memory trace" of the location of the visual stimulus (Duhamel, Colby and Goldberg, 1992). Though this anticipatory activity has not been studied explicitly in conditions evoking top-down spatial attention, predictive activity is greater for stimuli with greater bottom-up saliency (Gottlieb, Kusunoki and Goldberg, 1998; Joiner, Cavanaugh and Wurtz, 2011) and for stimuli that are learnt visual search targets (Phillips and Segraves, 2010; Mirpour and Bisley, 2012) or saccade targets (Gottlieb, Kusunoki and Goldberg, 1998). We hypothesize that the anticipatory remapping seen in attentional and oculomotor control areas like LIP, FEF and SC is part of the process that enables attentional remapping in MT that is well synchronized to the saccade. In other words, even though this process starts before the saccade in these areas, its effects in MT, with which these areas are strongly connected (Maunsell and van Essen, 1983; Ungerleider and Desimone, 1986; Blatt, Andersen and Stoner, 1990), only manifest after the saccade. In this view, the previous results on trans-saccadic remapping represent the predictive, pre-saccadic shift of attentional pointers on a retinotopic map that keeps track of attended locations across saccades (Cavanagh, Hunt, Afraz et al., 2010), so that attended locations can be preferentially processed with minimal delay after the saccade (Yao, Treue and Krishna, 2016). This reduction of delay would be especially helpful when planning rapid sequential saccades and could also help maintain an uninterrupted visual experience across saccades.

Though we did not find predictive remapping in MT, we did find evidence for a post-saccadic remapped response (i.e. a memory trace) in MT. To do this, we designed a new remapping paradigm that was different from the traditional one and recorded neuronal activity. The monkeys in this study were required to perform a task very similar to the first study, i.e. making a saccade while the fixation point jumped and responding to the motion change of a target stimulus (moving in the preferred or anti-preferred direction of the recorded neuron) while ignorinig distractors. The target stimulus could be in the RF or out of it in different conditions. In a very important condition, the stimuli were removed just before the saccade onset so that it never appeared in the neuron's RF. The responses in this condition enabled us to look for the presence of a remapped response, and ask if the remapped response was modulated by top-down attention and whether it contained information about visual features (motion direction in our study). We found evidence for a memory trace, in MT. The memory trace was modulated by top-down spatial attention: i.e. the neuronal response after the saccade signaled whether a target or a distractor stimulus

was present in its RF before the saccade. This was the first demonstration, to our knowledge, of the top-down attention influence on remapping activity. We also investigated whether the memory trace contained information about motion direction. We found only a small and transient effect of motion direction on the memory trace in only one monkey, suggesting that the remapped response did not signal the motion direction of the stimulus in the RF before the saccade. These data on the memory trace in MT contribute to an ongoing debate regarding the functional role of trans-saccadic remapping. The presence of feature-related information in the remapped response has become a critical test that distinguishes between two alternative views of the functional role of trans-saccadic remapping that are being actively debated (Wurtz, 2008; Cavanagh, Hunt, Afraz et al., 2010; Mayo and Sommer, 2010; Melcher, 2010; Zirnsak and Moore, 2014). Absence of featural information in the remapped response would support the proposal (Cavanagh, Hunt, Afraz et al., 2010) that trans-saccadic remapping represents the predictive, pre-saccadic shift of attentional pointers on a retinotopic map that keeps track of attended locations across saccades. On the other hand, the presence of featural information in the remapped response would support the proposal that trans-saccadic remapping plays an additional role in spatiotopic feature comparison and adaptation transfer across saccades (Melcher and Colby, 2008; Mayo and Sommer, 2010; Melcher, 2010; Crapse and Sommer, 2012), Our data from MT clearly support the former proposal. We propose that the memory trace emerges from the rapid shift of attention to the post-saccadic neuronal population and the resultant enhancement of the baseline firing-rate. The absence of motion-direction information in the memory trace is consistent with a shift of a purely spatial, top-down attentional signal. However, more data from different visual areas (including those in the ventral stream) are needed to fully decide this debate.

In summary, the physiological data presented here, combined with our human psychophysics results support our hypothesis that spatial attention and saccadic processing co-ordinate well to ensure that relevant locations are attentionally enhanced soon after the beginning of each eye fixation, and can be tracked and rapidly processed across saccades.

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