Neural Mechanisms of Implicit Visual Probability Learning

Philip Tseng,1,2 Hui-Yan Chiau,1,2,3 Chia-Lun Liu,1,2,3 Tzu-Yu Hsu,1,2,3 Chi-Fu Chang,1,2 Chang-Mao Chao,1,2,3 Wei-Kuang Liang,1,2 and Chi-Hung Juan1,2

1 Institute of Cognitive Neuroscience, National Central University
2 Laboratories for Cognitive Neuroscience, National Yang-Ming University
3 Institute of Neuroscience, National Yang-Ming University

Predictive information exists ubiquitously in the visual environment. Such information signals the probability or likelihood of upcoming events, thus facilitating the visual system in preparing optimal responses in advance. This ability of the visual system to implicitly acquire predictive and probabilistic information has been well documented by behavioral evidence from many domains (e.g., spatial, temporal, and abstract probability). Recently, neurophysiological studies have begun to elucidate the neural mechanisms underlying these learning processes and suggest a critical involvement of the fronto-parietal network and medial temporal lobe. In this paper we review evidence for such learning at the visual attention and oculomotor control levels. We also review some of the studies that delineate the neural substrates that contribute to probability learning at both levels: including the frontal eye field, supplementary eye field, posterior parietal cortex, and medial temporal lobe. Together, each of these regions provides a unique and critical contribution to probability learning in visual attention and oculomotor control.

Keywords: visual attention, probability, predictability, eye movements, transcranial magnetic stimulation (TMS)

Regularities can be found ubiquitously in our visual world. Take traffic lights, for example; there is a serial order for which signals light up (temporal), as well as the color (feature based) and location (spatial) of each light, thus reflecting regularities in several domains of one’s daily life. This information can be fully predictive of future events if they are always 100% valid, such as the traffic light. But even with partial predictive power (not always 100% valid), which we refer to as probabilistic, it remains advantageous to pick up such information, as the knowledge of any regularities can help the visual system reduce its computational load because future events can be anticipated and better managed in advance. Indeed, several studies have demonstrated the visual system’s capability to learn and exhibit knowledge of regularities in the environment with and without subjective awareness (e.g., Chun & Jiang, 1998; Fiser & Aslin, 2001; Geng & Behrmann, 2005; Kristjánsson, Chen, & Nakayama, 2001; Nakayama, Maljkovic, & Kristjánsson, 2004). Eye movement studies have also shown that people can direct their eyes and attention to highly probable locations faster than to low-probability locations without employing an
explicit strategy to do so (e.g., Farrell, Ludwig, Ellis, & Gilchrist, 2009; Liu et al., 2010, 2011).

The idea of the human brain being able to implicitly learn regularities is not new. The pioneering studies by Reber (1967, 1969) investigated whether people can extract hidden rules from strings of letters and generalize such rules to other letter combinations. The participants studied nonsense letter strings and were given a surprise test at the end. Most participants did not realize there were any kind of rules hidden behind the seemingly random letters. However, when they were shown new combinations of the studied letters, participants were able to guess whether or not the new strings had followed the hidden rule (which they did not explicitly know) above chance level (77% vs. 50%). This line of research clearly demonstrated that implicit learning can indeed occur without subjective intention and awareness.

This paper will focus on the same type of implicit learning in the visual domain. Most importantly, we will review evidence suggesting that such learning can be detailed enough to be sensitive to the differential likelihood of each event. Much like Reber’s findings, implicit learning in vision also involves extraction of hidden regularities, rules, or probabilistic information in the external world (e.g., Chun, 2000; Fiser, Berkes, Orbán, & Lengyel, 2010). That is, the visual system can pick up subtle associations and probabilities between objects or event occurrences and use such knowledge to aid task performance, with or without subjective awareness.

**Probabilities in Visual Attention**

Much of the work on visual learning at the attentional level was done using spatial predictability. One of the most compelling examples came from Chun and Jiang (1998), a phenomenon called contextual cuing. Contextual cuing describes a facilitative cuing effect that comes from the implicit recognition of the surrounding context. These authors designed a visual search paradigm and instructed participants to search for a target (a rotated T pointing either to the left or right) among many distracters (various rotated Ls). Unbeknownst to the participants, half of the trials would contain the same target-distracter spatial configurations (the old condition), and the remaining trials would contain new configurations (the new condition). Critically, target locations were held equal between the old and the new conditions; thus any learning effect cannot be attributed to repeating target locations. Target identity was 50:50 between a left- or right-rotated T so that any facilitation cannot be attributed to an associated response with a particular distracter configuration. Therefore, the only way to perform better in the old condition is to learn the statistical regularity of the distracter configuration, which provides a reliable cue to target location (but not identity). This was exactly what Chun and Jiang found. As the experiment progressed, participants’ reaction times (RT) were faster and declined more rapidly in the old condition, suggesting that participants had learned the spatial regularities of the repeating contexts. When asked to identify an old distracter layout from three other new layouts, participants performed at chance, suggesting such learning was indeed implicit. To rule out the possibility of a high response criterion, these authors in their subsequent study (Chun & Jiang, 2003) instructed their participants to guess the target location among the original target and distracter locations. Participants’ guessing rate still remained at chance level, although the learning and facilitation can remain durable and implicitly accessible for at least a week. Again, this effect demonstrates the visual system’s remarkable ability to extract hidden rules in spatial regularity and use it to aid visual search.

How does probabilistic learning play a role in the effects of implicit spatial learning such as contextual cuing? In other words, are highly-probable events learned better than less-probable ones even when such learning is implicit and incidental? To answer this question, Tseng and colleagues (Tseng, Hsu, Tzeng, Hung, & Juan, 2011) employed the original contextual cuing paradigm and systematically varied the frequency of appearances of the old contexts such that some contexts would appear three times within a block, and others twice or once. Target locations and their associated frequencies were matched between the old and the new condition. This was done to ensure that any improvement in the old condition
over and above the corresponding probabilities in the new condition could be attributed solely to the memory strength associated with each probability (e.g., high-frequency context in the “old” condition vs. the same high-frequency context in the “new” condition). These authors found overall contextual cuing effects in the old condition. Most important, the magnitude of facilitation improved as the probability increased (Figure 1). This suggested that implicit learning behaved much like explicit learning in the sense that its facilitative effect also varied as a function of its associative strengths. It is important to note that the predictive context is facilitative by efficiently directing eye gazes towards the target location (Neider & Zelinsky, 2006; also see Kunar, Flusberg, Horowitz, & Wolfe, 2007, for an effect in response selection). Indeed, Peterson and Kramer (2001) monitored participants’ eye movements and found that fewer saccades were made when context was repeated, suggesting a more efficient allocation of attention to the old condition. Thus, probabilistic information has a direct impact on visual attention and eye movements, suggesting a critical involvement of the frontoparietal attentional network that is also heavily involved in oculomotor control. To investigate this issue, our laboratory has conducted several experiments to trace the neural mechanisms of probabilistic learning (Chao et al., 2011; Chiau et al., 2011; Liu et al., 2010, 2011).

The frontoparietal attentional network is comprised of the frontal eye field (FEF) and the posterior parietal cortex (PPC), which includes the superior parietal lobule (SPL) and intraparietal sulcus (IPS), all of which are highly critical to the orientation of visual attention. We begin with the PPC, especially in the right hemisphere, whose role in the network includes visuomotor control (Ellison & Cowey, 2006; Morris, Chambers, & Mattingley, 2007; Nobre et al., 1997), updating spatial mapping (Andersen, Essick, & Siegel, 1985; Merriam, Genovese, & Colby, 2003; Morris et al., 2007), and shifting spatial attention (Chambers, Payne, Stokes, & Mattingley, 2004; Constantinidis & Steinmetz, 2005; Ellison, Rushworth, & Walsh, 2003; Mevorach, Humphreys, & Shalev, 2006; Schenkluhn, Ruff, Heinen, & Chambers, 2008). Damage to the right PPC may lead to hemifield neglect, where patients become unaware of the contralateral visual space although their visual acuity is not affected (Heilman & Van Den Abell, 1980; Mesulam, 1981).

Recently, studies have begun to discover that the attentional orientation function of PPC is highly dependent on probabilistic information in the environment (Konen, Kleiser, Wittsack, Bremmer, & Seitz, 2004).

Figure 1. Stimulus and results of contextual cuing from Tseng et al. (2011). Panel A shows a standard visual search array used in contextual cuing studies. The target (horizontal T) can point either left or right, even in repeating trials. Thus, the context (distractor layout) can only cue the location of the target, but not identity, thereby forcing the visual system to learn context instead of merely associating one context with one response. Panel B shows how frequencies of the context facilitates performance in a linear fashion.
especially when it is associated with rewards (Yang & Shadlen, 2007). To continue our discussion on the phenomenon of contextual cuing, Schankin and Schubö (2009) measured event-related potentials (ERP) using this paradigm and found greater negativity in the posterior parietal region around 200 ms after display onset. This component is known as the N2pc component (Luck & Hillyard, 1995), which reflects the allocation of visual attention in the parietal region that is contralateral to the attended stimulus. This physiological evidence demonstrates an important correlation between attentional allocation and the parietal cortex, as revealed through contextual probabilities. To establish causal evidence to confirm PPC’s role in processing probabilistic information, one of our recent studies (Chao et al., 2011) probed how predictive and non-predictive information can modulate PPC activity. In this study, *saccade curvatures*, along with saccade latency and accuracy, were recorded as they have been shown to be indicative of the active excitation and suppression processes that the visual system must resolve between the target and the distractor (e.g., McSorley, Haggard, & Walker, 2009; Walker, McSorley, & Haggard, 2006). Not surprisingly, people could saccade faster and with more precision and smaller curvature (less “pulling” effect from the distractors) when the target location was predictable. The pattern becomes interesting when we applied transcranial magnetic stimulation (TMS), a noninvasive neurostimulation technique that interferes with task performance by introducing noises to neural activity of the stimulated area, over the right PPC. When target location was predictable, PPC TMS had no significant effect on saccade curvature. However, when target location was unpredictable, TMS over the right PPC decreased saccade curvature towards the distractor such that interfered PPC functioning actually strengthened distractor suppression (Figure 2). These results suggest that PPC plays an important role in attentional capture (thus why PPC TMS would decrease attentional capture toward the distractor), but most important, that such attentional reorienting processes from the PPC are sensitive to predictive cues in the environment. Indeed, monkey neurophysiology has already shown that lateral intraparietal cortex (LIP, equivalent to the vicinity of human PPC) can encode behaviorally relevant objects (Gottlieb, Kusunoki, & Goldberg, 1998) and even the color of a cue if it is associated with an eye movement (Toth & Assad, 2002). In addition, target predictability can have a significant effect in modulating LIP activity (Konen et al., 2004). Yang and Shadlen (2007) also reported that neural activity in LIP can represent predictive information such as the weighted likelihood that certain shape combinations can lead to reward. Therefore, PPC is not only crucial to spatial attention, but may also be involved in processing meaningful information that is predictive of future events.

Besides spatial attentional reorientation, there are possibly other ways by which the right PPC is involved in

![Figure 2. Effect of TMS on PPC in predictable and unpredictable contexts, from Chao et al. (2011). The Y axis denotes the range of saccade curvatures, where negative numbers indicate less curvature towards the distractor. Panel A shows that PPC TMS decreased saccade curvature towards the distractor when distractor location is unpredictable, whereas Panel B shows that PPC TMS had no effect when distractor location can be predicted in advance. This suggests a critical role for the right PPC in attentional capture, and how predictability can modulate PPC involvement.](image-url)
processing predictive information. After all, probabilities exist in many forms beyond simple spatial layouts, and therefore cannot be entirely explained by spatiotopic representations of probabilities. Recent neuroscientific findings have suggested that the right PPC is also critical to the early encoding processes that support visual short-term memory (VSTM; Todd & Marois, 2004, 2005). This is important because probabilistic information, even if implicit, requires a mediating buffer to store and consolidate the newly-encoded information. To investigate whether the right PPC is really critical to the early encoding processes of visual information, our laboratory used a change detection paradigm that required the use of VSTM (Tseng et al., 2010). A change detection task presents two slightly-different images in succession, separated by a blank image, with very brief durations (approx. 100-250 ms each frame). The idea is that visual disruptions such as saccades, blinks, or a blank image in this case, would take away the salient motion signals that we often rely to detect changes, thus forcing people to commit information into their VSTM for change detection. In this context, it is necessary to encode and hold the items from picture A in VSTM, and successfully compare the stored items with those of picture A’ in order to ensure accurate change detection. Therefore, there is a serial order of stages that starts with encoding and maintenance, and ends with retrieval and comparison. Failure in any of these steps would result in poor detection performance. To investigate the role of the right PPC in these stages, we again applied TMS over the right PPC. We found that PPC TMS only impaired change detection when it was applied during the presentation of the first image, and had no effect when applied with the second image. This implies that the right PPC is important to the encoding processes when one views a scene or image, and is relatively less involved in the processes of retrieval and comparison. This encoding function of the right PPC provides an appropriate platform for learning probabilistic or predictive information at a higher level of visual processing.

Another region that is critical to implicit learning is the medial temporal lobe (MTL), including the hippocampus, parahippocampal cortex, and perirhinal cortex. These areas are well known for their role in conscious declarative memory (Aggleton & Brown, 1999; Cohen & Squire, 1980; Moscovitch, 1995; Squire, Stark, & Clark, 2004; Tulving & Schacter, 1990; Yonelinas, 2002), but later studies have suggested that it too can be involved in implicit learning of visual context (Eichenbaum, 1999; Eichenbaum, Otto, & Cohen, 1994). For example, fMRI studies have shown hippocampal activation in contextual cueing (Greene, Gross, Elsinger, & Rao, 2007). In contrast, amnesia patients with MTL damage, or healthy participants administered with midazolam that produces short-term amnesia, fail to show implicit facilitation of contextual cueing (Chun & Phelps, 1999; Park, Quinlan, Thornton, & Reder, 2004). Presentation of subliminal image pairs also activates the hippocampus despite the absence of conscious recognition (Degonda et al., 2005). The strongest evidence perhaps comes from a recent study by Hannula and Ranganath (2009). These authors presented their participants with 216 single face-scene pairs, and tested memory for these with using multiple choice testing. MTL activity was observed even when participants knew the answer but failed to consciously detect it, indicated by their eyes lingering around the correct choice longer than the wrong alternatives. Thus the results suggest that MTL can mediate implicit learning in the absence of conscious awareness. Interestingly, these authors also observed strong activation in prefrontal cortex (PFC), but only when participants consciously choose the right face. Thus, despite the common activation in MTL, activation of PFC is necessary to enable explicit recollection. Indeed, PFC activation has been consistently observed in complex probabilistic learning of categories (Fera et al., 2005; Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; Rushby et al., 2011; Weickert et al., 2009), and is associated with focused attention and explicit change detection (Fernandez-Duque, Grossi, Thornton, & Neville, 2003), evaluating remembered information with respect to a particular behavioral goal (Dobbins & Han, 2006), and guiding explicit associative memory decisions (Duarte, Ranganath, & Knight, 2005).
Probabilities in Oculomotor Control

Aside from probabilistic learning in the domain of high level visual cognition (e.g., attention, memory, etc.), much of the work on probabilistic learning has been done in the context of directing eye movements to different spatial locations. We refer to this implicit control of saccadic behavior as oculomotor control, which receives processes information from the retina at a time point that is earlier than high level visual attention and memory. As such, the underlying neurophysiology of these probabilistic saccadic behaviors is better understood, in part due to the contribution of animal models, and thus provides an excellent model for studying the flexibility of human behaviors. Miller (1988) studied the effects of absolute and relative target position. A target letter was to be detected in a sequence of four letters in which one location had a higher probability of containing the target. The letter sequence was occasionally offset in horizontal position to probe whether the effects of high probability was dependent on absolute position or the position in the sequence (relative position). It was found that target location probability benefited from both types of spatial relationship. Later studies by Geng and Behrmann (2005) investigated the role of targets’ spatial probabilities in a visual conjunction search task and found that spatial probability is independent of any benefit afforded by the explicit endogenous cue (the effect was purely additive) but interacted with the salient exogenous cue. Thus, the probability cue perhaps operated through a conjunction of spatial and object information and was processed within a system shared by explicit spatial cues.

How do these external regularities affect human saccadic behaviors? To explore this issue, we investigated whether the probability effects can be extended to the pro-and antisaccade task to elucidate the dynamic mechanisms of cognitive flexibilities in humans (Liu et al., 2010). Prosaccade and antisaccade refers to eye movements toward (pro) or away from (anti) the target, and have been consistently found to have shorter and longer RT, respectively, due to the extra stages of suppression in antisaccades (termed the antisaccade cost; Everling & Fischer, 1998; Kristjánsson, 2007; Kristjánsson et al., 2001; Kristjánsson, Vandenbroucke, & Driver, 2004; Munoz & Everling, 2004; Olk & Kingstone, 2003). In this study, we used an orienting paradigm with varying location probabilities (Figure 3) to investigate how probabilistic information may modulate the RT difference between pro- and antisaccade even though participants are not aware of such probabilistic manipulation. We found that under these conditions, prosaccades to the probabilistically-salient location became faster. The sizes of the antisaccade cost also changed to compliment the magnitude of prosaccade probability. Most important, like Tseng et al.’s study (2011), the saccade RTs followed the magnitude of probability saliency such that the RTs decreased gradually as the probability of a certain location increased, and vice versa (Figure 4). Together, these results suggest that the oculomotor system is sensitive to multiple levels of spatial probability in the absence of participants’ awareness.

Figure 3. The spatial orienting paradigm used in Liu et al. (2010, 2011). Participants were shown a central disc that cued either a prosaccade or antisaccade. This paradigm is able to manipulate levels of probability in prosaccade locations but not antisaccade locations. Behavioral results suggested that these two types of saccades can indeed be dissociated since the effect of probability in prosaccade is not transferred to the same location in an antisaccade.
The neural mechanisms of probabilistic learning at the oculomotor level involve a network of brain regions. Specifically, the superior colliculus (SC), supplementary eye field (SEF), and frontal eye field (FEF) tend to produce pretarget-related neural activity during saccade preparation (SC: Basso & Wurtz, 1997, 1998; Dorris, Paré, & Munoz, 1997; SEF: Connolly, Goodale, Goltz, & Munoz, 2005; Schlag-Rey, Amador, Sanchez, & Schlag, 1997; Stuphorn & Schall, 2006; FEF: Bichot & Schall, 2002; Sato & Schall, 2003; Schall, 1997). In SC, Basso and Wurtz (1997) first described how the firing rate buildup of neurons in monkey superior colliculus was reduced when previous task experience (probability) increased the certainty of a target location. Dorris and Munoz (1998) also studied how saccadic reaction times and buildup of neuronal activity in monkey superior colliculus were affected by probability. Specifically, when saccades were directed to a particular receptive field more frequently, the firing rates of the neurons for that particular receptive field would become higher before the initiation of each saccade. These results suggest that the probabilities of saccadic locations can modulate the buildup of neuronal activity, which consequently leads to our aforementioned observations (Liu et al., 2010).

In FEF, Sato and Schall (2003) found 2 types of neurons in macaque monkeys that selectively responded to either the singleton regardless of the ultimate gaze shift (target selection) or the saccade endpoint regardless of singleton location (saccade selection). The latter group of neurons could account for the different saccadic reaction times (SRTs) for these 2 types of response because these neurons had to select saccade endpoints depending on the trial type (i.e., prosaccade or antisaccade). This demonstrates that the 2 types of neurons can correspond to sequentially distinct visual processing, such as target and saccade selection. Indeed, two studies from our laboratory (Juan et al., 2008; Juan, Shorter-Jacobi, & Schall, 2004) have confirmed that attention (target visual analysis) and eye movements (saccade preparation) are two independent stages of processing within FEF that can be dissociated from each other. Therefore, the effect of probability learning can possibly occur in either one of the stages, or both. Indeed, in the first study, Juan and colleagues (Juan et al., 2004) applied intracranial microstimulation in FEF in monkeys at different stages of a saccade and found that saccades can deviate towards the endpoint location instead of target locations when the two do not match, suggesting that covertly orienting attention is possible without preparing a saccade (Figure 5). Therefore the role of FEF in mediating the effect of probability is not simple as probabilistic information can exert its influence either at the attentional level or the saccade preparation level, which both heavily rely on FEF.

In the second study, Juan et al. (2008) incorporated unpredictability into their orienting paradigm by interleaving the pro- and antisaccade trials within one block. Saccade type was dependent on the randomized orientation of the target singleton. As such, identification of the orientation of a singleton was required to continue saccade preparation. This manipulation was able to eliminate the antisaccade cost because saccade types were no longer predictable. This unpredictability can be viewed as a 50:50 uncertainty in probability between pro- and antisaccades, which we discuss in more detail later (Chiau et al., 2011). In this study, TMS was delivered over FEF to probe the time course of the involvement of this area in performance of the antisaccade task. In prosaccades,
we found that early (target selection) and late (endpoint selection) TMS both were able to disrupt task performance (Figure 6). The two distinct time windows suggest that target analysis and saccade preparation, although both occurring in FEF, are not likely to be originated from the same process, which replicates our findings from the first study. Together, these studies suggest that FEF is critical to the processes of target selection and saccade preparation, which makes FEF a plausible region for mediating the effect of probability learning. In addition, preparatory-related activities can be found in FEF with trained monkeys in an antisaccade task, and these signals in their unaltered form are sent directly to the SC (Everling & Munoz, 2000). fMRI data also showed that FEF activity can be used to predict SRT in humans (Connolly et al., 2005). Thus, these findings suggest that the effect of location probability on SRT could be reflective of the neural firing rate within a subpopulation of neurons in the FEF. This may account for the role of FEF in mediating the effects of location probability because both target and endpoint selections are necessary for the benefit of location probability to surface.

Figure 5. The orienting paradigm and results from Juan et al. (2004). The target singleton’s orientation cued whether a prosaccade or antisaccade should be performed (Panel A). Therefore, covertly orienting attention to the singleton is needed in order to determine saccade type as shown in Panel B. In prosaccade trials, most neurons in FEF activated when the saccade endpoint was where the singleton was located (left). In contrast, for antisaccade trials most neurons activated to the singleton first then selected the endpoint (right). This paradigm therefore dissociates attention from eye movements. Furthermore, it is uncertain whether the antisaccade would deviate towards the singleton (location of orientation analysis) or the endpoint (location of antisaccade endpoint). Intracranial microstimulation was applied in three different time windows, as Panel B and C labeled with 1, 2, and 3. Most important is the time window 2 where singleton analysis has been completed but saccade selection has not. The hypothesis is plotted in Panel D. The x axis and y axis are the timing of intracranial microstimulation and deviation to the location of singleton respectively. Positive angles denote deviations toward the singleton, and negative angles denote deviations away from the singleton. The results showed that antisaccades (right) deviated towards the saccade endpoint, where the eyes should move, instead of to where attention is allocated.
The involvement of SEF in probabilistic oculomotor control is less clear. On one hand, the SEF seems like a reasonable candidate to be involved in such learning process due to its roles in conditional oculomotor learning (Chen & Wise, 1995; Olson & Gettner, 2002), reward or error monitoring (Roesch & Olson, 2003; Stuphorn, Brown, & Schall, 2010), smooth pursuit (Nyffeler, Rivaud-Pechoux, Wattiez, & Gaymard, 2008), and antisaccades (Curtis & D’Esposito, 2003; Schlag-Rey et al., 1997). However, a direct test was needed to confirm a critical role for SEF in probabilistic learning in the context of an orienting paradigm. To this end, we conducted a follow-up TMS study (Liu et al., 2011) based on the Liu et al. (2010) paradigm. Using the same orienting paradigm and manipulation of probability (75% prosaccades are directed to one location while antisaccades remain evenly distributed), we applied theta burst TMS over participants’ FEF or SEF for 20 seconds (Figure 7). This offline approach to TMS noninvasively interferes with neural activities for a prolonged period of time (~20 min), thus directly tests for a causal relationship between a specific brain region and a behavioral pattern. Interestingly, we found that FEF TMS successfully disrupted the effect of probability such that high-probability prosaccades became slower when TMS was applied. In contrast, SEF TMS did not slow

![Figure 6. FEF TMS effects on the saccade latencies of pro- and anti-saccades were found in two distinct time windows suggesting that the stages of visual selection and motor preparation can be temporally separated in FEF, results from Juan et al. (2008). Panel A shows a significant effect of early TMS timing on prosaccade latency. Post hoc comparisons showed that this was due to increased latencies when TMS was delivered starting at 40 ms following array onset. Elevated latencies were not significant for antisaccade trials (it is possibly due to containing two populations of responses) in the early TMS time window. For later TMS delivery times (panel B), both pro- and antisaccade latencies were significantly increased by TMS prior to but not during saccade execution.](image-url)
These results suggest that FEF, but not SEF, is critical to the learning of spatial probabilities in this orienting paradigm (Figure 8). This finding is surprising due to the reasons outlined above that make SEF a good candidate for probability learning. Therefore, we think SEF may still be involved in probabilistic learning, but in other forms beyond spatial probabilities. This may include more abstract associations such as temporal or event probability (e.g., ratio between pro- and antisaccades, but not tied to a particular location). To this end, we conducted a study that demonstrates how event probability can also powerfully modulate saccadic behaviors (Chiau et al., 2011), which we describe in more details below.

Event probability is quite different from what we have covered so far. Unlike spatial probability, event probability is more abstract because it does not require a spatially predictive component. Instead, it is the tracking of a specific patterns of behavior (e.g., performing the same specific type of saccade, although to different locations) over time. The Juan et al. (2004) study has demonstrated that a 50:50 uncertainty, or the lack of predictive probability, can eliminate the antisaccade cost because the environment no longer favors one type of saccade over another. Following this logic, it is reasonable to assume that antisaccades should produce an advantage instead of a cost in SRT when external probability favors antisaccades over prosaccades. To test this possibility, Chiau and colleagues (2011) interleaved pro- and antisaccades, but gradually changed the ratio between the two saccade types from 80:20 to 50:50 and 20:80 while participants were performing the orienting task. None of the participants explicitly noticed the change of ratios, but their SRTs accurately reflected the favored probability at the time. That is, participants performed prosaccades faster than antisaccades when prosaccades were favored (80:20); no antisaccade cost when probability was held equal (50:50); and most important, faster antisaccades than prosaccades (antisaccade advantage) when probability was reversed to favor the execution of antisaccades (20:80). This type of probability learning is not a simple association between saccade and spatial locations because each interleaved pro- and antisaccades always have four possible endpoints. Thus, the stage of processing that most likely benefits from external probability is the saccade preparation stage; because it is implausible that common processes (shared by both saccade types) such as visual analysis of target orientation would produce such a bidirectional pattern. This was confirmed by a second experiment when the authors introduced three levels of difficulty in target discrimination: Overall saccade latency was increased in both pro- and antisaccades, but the antisaccade cost still changed as a function of trial type probability rather than discrimination difficulty. These findings suggest that the effect of trial type probability on antisaccade cost is likely to have originated from the saccade preparation process, and not visual discrimination.

If event probability benefits the processes in the saccade preparation stage, then the mechanisms behind such learning should be similar to probability priming, where the endpoints of the probable saccade type enjoys a lower threshold or early neural activity buildup (Connolly et al., 2005; Dorris & Munoz, 1998; Dorris, Paré, & Munoz, 2000; Everling & Munoz, 2000), which speeds up the process of saccade preparation and thus decrease saccade latency. In contrast, the less probable saccade type not only misses such facilitation, but has to inhibit
and override those pre-established neural responses that favor the likely saccade type, and reselect a new endpoint. Based on the previously-reviewed literature, this facilitation seems to involve FEF (Liu et al., 2011; Sato & Schall, 2003). However, the FEF neurons prefer a specific retinotopic endpoint for saccades, yet this study does not rely on spatial probabilities. Instead, event probability of saccade type relies on the symbolic meaning of an abstract instruction rather than on spatial locations. Thus, we think SEF, with its direct projection to FEF and SC, may be a key candidate here due to its ability to modulate FEF and SC activity (Schall, Morel, & Kaas, 1993; Shook, Schlag-Rey, & Schlag, 1990). It is possible that the effects of probability first take place within SEF, which then sends its outputs to oculomotor control areas like FEF and SC. The probabilistic representations in SEF may directly benefit the selection processes of FEF by increasing the motor preparation level near threshold, which would decrease saccade latency as a result (Connolly et al., 2005; Connolly, Goodale, Goltz, & Munoz, 2002; Hanes & Schall, 1996; Koval, Ford, & Everling, 2004; Monoach et al., 2007). Neurophysiological evidence comes from several studies. For example, Schlag-Rey and colleagues have found that SEF neurons consistently fire more rapidly before antisaccades instead of prosaccades (Amador, Schlag-Ray, & Schlag, 2004; Schlag-Rey et al., 1997). Cortical potential studies conducted by Everling, Krappmann, and Flohr (1997) also observed larger negativity in SEF before antisaccades. Furthermore, fMRI studies found that SEF showed larger activation during the preparatory period (e.g., Brown, Vilis, & Everling, 2007; Curtis & D’Esposito, 2003) on antisaccade trials than on prosaccade trials. Future studies that directly test the link between SEF and abstract probability are much needed.

Figure 8. FEF TMS modulates the location probability effect on saccade latency, results from Liu et al. (2011). Mean saccadic RTs as a function of TMS, saccade type, and probability. The top two panels indicated FEF and SEF TMS conditions respectively. In FEF TMS condition, the pattern of the location probability effect was affected by TMS and also the general saccade latencies were increase. In the SEF TMS condition, none of the effects were influenced by TMS. Error bars represent the standard error of the mean. Panel B shows how right FEF TMS decreased SRT in prosaccades to the high probability location, suggesting a critical role for the right FEF in mediating the effect of spatial probability. This effect was not observed in the SEF TMS condition.
Conclusion

In this paper we have briefly reviewed how predictive, or probabilistic, information in the environment can powerfully modulate human visual attention and oculomotor control. This type of learning can often be implicit, and exists in both spatial and abstract domains. Neurophysiological studies suggest that such learning requires a dynamic interplay between regions within the fronto-parietal network, which includes PPC, FEF, and SEF, as well as the MTL. Much of the work until now has emphasized the individual contributions of these regions to mediate probability learning. Future studies that disentangle the timing, roles, and interactions between these regions will provide exciting new insights into how the visual system strategically adapts to the environment.

References


Schlag-Rey, M., Amador, N., Sanchez, H., & Schlag, J. (1997). Antisaccade performance predicted by neuronal...


內隱性視覺機率學習的神經機制

曾祥非¹ ² 喬慧燕¹ ² ³ 劉嘉倫¹ ² ³ 徐慈妤¹ ² 張期富¹ ² 趙長懋¹ ³ 梁偉光¹ ² 阮啟弘¹ ²
¹國立中央大學 認知神經科學研究所
²國立陽明大學 認知神經科學實驗室
³國立陽明大學 神經科學研究所

在視覺所及之處，預測性訊息無所不在。這些訊息預告著隨即發生的事件機率及可能性，讓視覺系統得以事先準備，並用最有效的狀態反應。這類事先獲取資料訊息的內隱性處理過程，在諸多研究領域中已受到許多行為證據支持證明（如：空間、時序、抽象機率）。近年來，神經生理學也試著去了解這些學習過程背後的神經機制。其結果顯示額葉及頂葉網絡和內側顳葉佔有不可或缺的角色。本文試回顧探討此類學習歷程在視覺注意力及眼球運動控制層面上的各種證據，並檢視現今研究之結果，以探討其神經機制。此研究議題所涉及之腦區包含額葉眼動區、輔助眼動區、後頂葉皮質及內側顳葉。總結各項發現，上述區域對於機率學習在視覺注意力及眼球運動控制的表現上皆有其關鍵且獨特的重要角色。

關鍵詞：可預測性、視覺注意力、眼球運動、跨顳極刺激、機率