

THEMATIC COLLECTION: INTRODUCTION

Cortical Indexes of Saccade Planning in Infants

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This article briefly reviews the development of cortical involvement in saccadic eye movement in young infants. A distinction between reflexive and voluntary saccadic eye movements is made, and developmental changes in the neural systems controlling these eye movements are discussed. Cortical indexes of saccade planning in adults have been measured using scalp-recorded, event-related potential (ERP). The ERP may be useful in distinguishing reflexive and voluntary saccadic eye movements in infants. In the remainder of this Thematic Collection, 3 studies are introduced that used ERP measures to infer saccade planning in young infants, and 2 short articles comment on these studies.

The shift of attention to different regions of space is generally accompanied by eye movements. Even though shifts of attention may occur without eye movements (e.g., covert orienting), processing of fine visual detail, color, and form are most easily done by the fovea. Thus, eye movements function to center the fovea on a new location or on a stimulus located in a new location. The eye movements that are used to move the eyes from one location to another are high-velocity saltatory jumps of the eyes called *saccades*. Saccades to new locations may be the result of unexpected stimuli occurring in a location or may be the result of planned shifts of attention. It is often assumed that very young infants' saccades are reactive to stimuli occurring in new locations and that planned eye movements do not occur in young infants. This article briefly reviews some background for this assumption

and introduces three articles that attempt to use cortical measures to study saccade planning in infants.

TWO EYE MOVEMENT SYSTEMS

There are two distinct brain systems that control saccadic eye movements. Schiller (1985, 1998) summarized neuroscience work on the primate visual system and eye movement control. Schiller described one brain system that controls reflexive saccades to the sudden onset of an unexpected peripheral stimulus. This system includes a brain pathway involving the retina, lateral geniculate nucleus, primary visual area, suprasylvian cortex, and superior colliculus. The superior colliculus, which is a subcortical structure located in the midbrain, has a topographical map of the spatial environment and produces activity that controls the direction and amplitude of the reflexive saccade. Schiller described a second brain system that controls saccades that are voluntary or planned. This brain system is affected by attention and may result in saccades that are directed to locations in space or saccades that are directed to targets. This system includes a brain pathway involving the retina; lateral geniculate nucleus; Visual Areas 1, 2, and 4; the parietal cortex area PG; and the frontal eye fields (FEFs). The FEFs have a topographical map of the spatial environment and produce activity that controls the direction and amplitude of saccades. The FEFs in each hemisphere affect eye movements contralateral to that hemisphere. The FEFs and superior colliculus control brain-stem areas that program the brain-stem motoneurons that cause the eye muscles to move the eye in its orbit. These brain-stem areas control saccade velocity. The FEFs may act directly on the brain-stem areas controlling brain-stem motoneurons or may act through the superior colliculus to initiate and direct saccadic eye movements.

DEVELOPMENT OF THE TWO EYE MOVEMENT SYSTEMS

What is the relevance of the two eye movement systems for infant development? There have been several models that have posited that the development of the neural systems involved in reflexive and voluntary saccades forms the basis for behavioral development observed in infants. These have included models by Bronson (1974), Maurer and Lewis (1979), Johnson and colleagues (Johnson, 1990, 1995; Johnson, Gilmore, & Csibra, 1998; Johnson, Posner, & Rothbart, 1991), Hood (1995; Hood, Atkinson, & Braddick, 1998), and Richards (Richards & Casey, 1992; Richards & Hunter, 1998). Of most interest to the three empirical articles following this one is Johnson's (1990, 1995; Johnson et al., 1998; Johnson et al., 1991) model. This model hypothesizes that the development of the primary visual area is

a controlling factor for the influence that the brain systems controlling eye movement may have on infant saccades. The primary visual area is a gateway for reflexive and voluntary eye movement systems. However, the pathways that control reflexive eye movement use a different layer of the primary visual cortex than the pathways controlling voluntary eye movements. Johnson (1990) also used in his model a direct projection from the retina to the superior colliculus that bypasses the visual cortex (although in humans this pathway is probably not heavily involved in reflexive saccadic eye movements; Richards & Hunter, 1998; Schiller, 1998). The reflexive eye movement pathway is relatively mature at birth, and Johnson (1990) hypothesized that saccadic eye movements in the first 2 to 3 postnatal months should be reflexive and controlled by the superior colliculus. The pathway controlling voluntary saccades uses layers of the primary visual cortex that are relatively immature at birth. These layers show rapid development over the first 6 postnatal months. Thus, attention-directed voluntary saccades should have a more protracted developmental trajectory than reflexive saccades.

A recent study illustrates the behavioral development of reflexive saccades and attention-directed saccades in infants from 2 to 6 months of age (Richards & Holley, 1999). This study used the tracking of a simple visual stimulus under conditions of attention and inattention, and used the electrooculogram to measure eye movements. Reflexive saccades used in visual tracking showed little or no development over this age range. Attention-directed saccades and smooth pursuit eye movements showed a dramatic increase over the age range of infants in the study. Of interest, with respect to this article, was attention-related saccadic tracking. The tracking stimulus was presented at differing speeds. When the older infants (4.5 and 6 months old) were attentive to the stimulus display, as the speed of the tracking stimulus became too fast for smooth pursuit eye movements to follow, the infants shifted from smooth pursuit tracking to saccadic tracking. Alternatively, when the infants were inattentive, their tracking performance decreased as the speed of the tracking stimulus increased. This implies that attention-directed eye movement systems (smooth pursuit, voluntary saccades) interact to perform visual tracking. The behavioral development in this study was consistent with the hypothesis that there was a change from primarily reflexive (subcortically influenced) saccadic eye movements at 2 months of age to voluntary (attentive, cortically influenced) saccadic eye movements over the first 6 months.

This model recently has been called into question by studies showing that infants make predictive eye movements at very early ages in the *visual expectation procedure*. The visual expectation procedure (Haith, Hazan, & Goodman, 1988) consists of the presentation of stimuli in a regular sequence, such as an alternating series (e.g., right–left–right–left). Infants at very young ages (e.g., 2–3 months) will make saccadic eye movements toward the upcoming stimulus location that anticipate its occurrence and will respond to the predictable location more quickly than to unpredictable locations. This has been interpreted as the infant forming an

expectation about the upcoming location and making a predictive saccade toward it. If predictive saccades are controlled by the frontal cortex (i.e., FEFs) then this would imply that saccades in the paradigm involve the cortical areas controlling voluntary saccades, and such FEF control happens much earlier than Johnson's (1990) model predicts. This interpretation has been forwarded by Wentworth and Haith (1998) and Canfield, Smith, and colleagues (Canfield, Smith, Brezsnayak, & Snow, 1997; Smith & Canfield, 2000).

CORTICAL SACCADE PLANNING MEASURED WITH EVENT-RELATED POTENTIALS

How may the two eye movement systems be distinguished in young infants? One approach to their measurement is the use of the event-related potential (ERP). The ERP is found by averaging the electroencephalogram (EEG) over multiple trials and time locking those averages to specific psychological or experimental events. The scalp-recorded EEG is caused by action potentials occurring in the cerebral cortex and thalamocortical connections. Therefore, the scalp-recorded ERPs are hypothesized to represent specific events occurring in the cortex (Hillyard, Mangun, Woldroff, & Luck, 1995; Swick, Kutas, & Neville, 1994). The ERPs relevant to saccadic planning would be found in ERPs that are time locked to the onset of the saccadic eye movement and averaged back in time before the event (presaccadic ERP). Significant presaccadic ERP components that are consistently related to saccades represent cortical activity closely related to the saccades. These presaccadic ERP changes may reflect cortical areas involved in saccade planning (Balaban & Weinstein, 1985; Csibra, Johnson, & Tucker, 1997; Csibra, Tucker, & Johnson, 1998; Johnson et al., 1998; Kurtzberg & Vaughan, 1980, 1982; Richards, 2000). The saccades that occur in the absence of specific presaccadic ERP activity are assumed to be controlled by subcortical neural systems.

Three types of EEG activity have been reported in adult studies of presaccadic ERP. First, an early negativity has been observed that begins up to 1 sec prior to saccade onset with maximum negativity at the vertex (Becker, Hoehne, Iwase, & Kornhuber, 1973; Kurtzberg & Vaughan, 1980, 1982; Moster & Goldberg, 1990; Thickbroom & Mastaglia, 1985a). This negativity is thought to reflect activation of the FEFs prior to saccade onset or motor potentials in the supplementary eye fields of the supplementary motor area. This negative presaccadic ERP occurs primarily when there is a relatively long (e.g., 1–2 sec) interval preceding the saccade, and the interval between saccades, or between stimuli to which saccades are made, is predictable. Second, a slowly increasing positive potential (slow wave) about 30 to 300 msec prior to saccade onset may sometimes be identified (Becker et al., 1973; Csibra et al., 1997; Kurtzberg & Vaughan, 1980, 1982; Moster & Goldberg, 1990; Thickbroom & Mastaglia, 1985a). This positive slow

wave occurs over the parietal cortex contralateral to the eye movement. Third, about 10 to 20 msec prior to saccade onset there is a positive *spike potential* in the ERP (Balaban & Weinstein, 1985; Becker et al., 1973; Csibra et al., 1997; Kurtzberg & Vaughan, 1980, 1982; Thickbroom & Mastaglia, 1985b; Weinstein, Balaban, & Ver Hoeve, 1991). As with the positive slow wave, the spike potential is largest over the parietal scalp leads (P3, P4) and is larger contralateral to the eye movement. These three presaccadic potentials also occur with antisaccades, which are saccades in the direction opposite to which a cue occurs. In the case of antisaccades, the presaccadic negativity is larger for antisaccades than saccades in the direction of the stimulus, whereas the presaccadic positivity and the spike potential are smaller in some recording locations for antisaccades than saccades of other types (Evdokimidis, Liakopoulos, Constantinidis, & Papageorgiou, 1996; Everling, Krappmann, & Flohr, 1997).

An interesting aspect of these presaccadic ERP changes is their relation to voluntary eye movements. One study of presaccadic negativity separated saccades into saccades to an unexpected stimulus, saccades to a predicted target location, and saccades back toward the predicted location of a previous fixation point (Evdokimidis, Mergner, & Lucking, 1992). The anticipatory saccades toward the predicted target location and the saccades back toward the previously fixated target site showed an early widespread negativity over the contralateral cortex and a negativity over the contralateral central lead (e.g., C3 or C4). The earliest widespread negativity was interpreted as reflecting response preparation, whereas the central contralateral negativity was interpreted as reflecting neural activity in the FEF or premotor cortex. The visually triggered reflexive saccades showed only a contralateral parietal activity fairly close to the saccade onset (30 msec). This presaccadic spike potential also occurs most frequently in voluntary rather than reflexive eye movements (Balaban & Weinstein, 1985). These findings are consistent with the position that significant presaccadic ERP components reflect cortical areas involved in saccade planning and are consistently related to voluntary and not reflexive saccades.

Two studies used presaccadic ERP changes in infants' eye movements. The first of these was by Csibra et al. (1998). They presented 6-month-old infants with a focal stimulus followed by a peripheral stimulus in a "gap" paradigm. The peripheral stimulus in one condition was presented simultaneously with the focal stimulus (overlap condition) or presented after a brief delay after the focal stimulus was turned off (gap condition). Adults in this paradigm showed a presaccadic slow wave activity and spike potential (Csibra et al., 1997). There was no evidence of the slow wave activity or the spike potential in the infant participants (Csibra et al., 1998). They concluded from this lack of presaccadic activity in the infant participants that the saccades toward the peripheral targets were under subcortical control (e.g., superior colliculus) and did not involve cortical saccade planning. The overlap and gap conditions in Csibra et al. (1997; Csibra et al., 1998) involved an exogenous cue in an unexpected location, and target location was unpredictable.

Thus, it is possible that the infants did not develop a specific expectation about target occurrence or location, and thus, the saccadic eye movements were controlled by the reflexive saccade system.

A second study examining presaccadic ERP changes in young infants was done by Richards (2000). The infants ranged in age from 3 to 6 months and were tested in a spatial cuing paradigm (Hood, 1995). In the spatial cuing paradigm, a cue is presented in a specific location followed by a target that either occurs in that location (ipsilateral or valid trials) or in another location (contralateral or invalid trials). Richards reported that a positive potential occurred over the contralateral frontal scalp areas about 50 msec preceding the saccade on the valid trials. This presaccadic activity did not occur in 3-month-old infants, was stronger in 4.5-month-old infants, and largest and more widespread in 6-month-old infants. This presaccadic activity was not present on the invalid trials or on the trials in which no cue was presented, and the infant made a saccade toward an unexpected target. These results were interpreted as indicating that the cue caused a covert shift of attention to the cued location and an expectation about the occurrence of a target occurring in that location. Cortical saccade planning was reflected in the presaccadic positive potential of the ERP. Alternatively, when the target occurred in an unexpected location, or no cue occurred, no expectation was developed, and saccades to the target were reflexive and unaccompanied by presaccadic ERP activity. The location of this scalp activity over the frontal areas contralateral to the saccade was interpreted as consistent with activity in the FEFs or sensorimotor eye fields controlling eye movements to a predicted target.

THREE STUDIES TESTING CORTICAL INDEXES OF SACCADE PLANNING IN INFANTS

The three studies following this article use presaccadic ERP changes as cortical indexes of saccade planning in young infants. Two short articles comment on these studies. Two of the studies (Csibra, Tucker, & Johnson, this issue; Wentworth, Haith, & Karrer, this issue) used the visual expectation procedure (Haith et al., 1988) and studied infants that were 3 months old (Wentworth et al., this issue) or about 4 months (18 weeks) old (Csibra et al., this issue). The visual expectation procedure presents stimuli in locations in a regular sequence. For example, a pattern may occur alternately on the right and left sides or in a sequence such as right–right–left. Infants will make anticipatory saccadic eye movements toward the upcoming stimulus location before the stimulus is presented. They also will respond more quickly to a predictable location than to an unpredictable one. This implies that an expectation has developed about the upcoming stimulus and suggests that the saccades occurring toward the expected location are planned rather than reflexive and, therefore, should involve cortical areas involved in voluntary saccades.

The findings of these two studies have similarities and differences. Both studies resulted in eye movements toward the stimuli that were anticipatory, indicating that the infants formed an expectation about the location of the upcoming stimulus and looked toward the location in advance of its presentation. The ERP findings were dissimilar in one respect and similar in another. Wentworth et al. (this issue) found for anticipatory saccades a positive potential about 30 to 90 msec before saccade onset in the frontal lead that did not occur for reactive saccades. Alternatively, Csibra et al. (this issue) found a positive ERP component at a slightly earlier time period (110 msec), and this occurred primarily in the Pz lead. The time frame and positive direction of these findings are comparable, but the location varies significantly. Both studies reported either a negative potential shift or a more negative ERP in frontal leads at about 500 msec before the anticipatory saccades. This presaccadic negativity was similar to what has been found in studies of adult presaccadic eye movements (Becker et al., 1973; Kurtzberg & Vaughan, 1980, 1982; Moster & Goldberg, 1990; Thickbroom & Mastaglia, 1985a). This presaccadic negativity may be related to planning of motor movements that would be expected to occur in cortically controlled planned saccades.

The third study (Richards, this issue) used 4.5-month-old infants in a spatial cuing paradigm (Hood, 1995; Richards, 2000). The spatial cuing procedure presents a cue in a location followed by a target in that location or another location. A covert shift of attention to the cue should lead to an expectation that a stimulus may occur in that location and result in planned saccades to the cued location and reflexive saccades to an uncued location (Richards, 2000). This third study and the Wentworth et al. (this issue) study found a similar presaccadic positive potential occurring before saccade onset. Both studies found a positive ERP component in frontal leads about 30 to 60 msec before a saccade. In Wentworth et al., this presaccadic positive potential occurred primarily for saccades that anticipated the onset of the peripheral stimulus. In Richards (2000), this positive potential occurred when infants made an eye movement to a target that was in the cued location. In both cases, the interpretation of this type of eye movement is that planning occurs in advance of the eye movement and that this eye movement was controlled by brain systems involved in voluntary eye movements. However, Richards (this issue) also found endogenous saccades that were made to the cued location in the absence of the target (prior to target onset or when no target was presented). These endogenous saccades were similar to the anticipatory saccades in the visual expectation procedure, because a saccade was made to an expected location in the absence of a stimulus. In this case, Richards (this issue) reported that the presaccadic positive potential did not occur, contrary to the finding of Wentworth et al. for anticipatory saccades.

Some differences between the three studies may have occurred because of the paradigms used to elicit the saccades. This is best illustrated in the stimulus-locked average potentials described in Wentworth et al. (this issue) and Csibra et al. (this issue). The Wentworth et al. study found a stimulus-locked ERP response of a neg-

ative slow wave and the Nc component. The time course of these stimulus-locked responses would overlap reactive eye movements occurring to the stimulus and potentially confound the presaccadic ERP potentials. Conversely, at stimulus offset there was a late-occurring, positive ERP response over the frontal electrode locations (Csibra et al., this issue). This ERP response was larger for subsequent saccades to the next stimulus when the saccade was reactive to the next location than when the saccade was anticipatory. Thus, the stimulus offset response, which may have overlapped the anticipatory but not the reactive saccades, may be affecting the presaccadic ERP response that was measured. If the onset-locked (Wentworth et al., this issue) or offset-locked (Csibra et al., this issue) ERP activity affects the characteristics of the presaccadic ERP activity, then the different methods used to elicit the visual expectations could affect the pattern of presaccadic ERP activity. This also is true for the Richards (this issue) study presented here, because the spatial cuing procedure used in that study results in onset-locked responses to the target (see Richards, 2000).

The use of presaccadic ERP in these studies is an attempt to measure cortical involvement in saccades. The close association of EEG and ERP with cortical activity would lead to the conclusion that the saccades occurring with a regular relation to ERP activity would be based on cortical systems. Alternatively, the lack of the time-locked EEG activity for saccades would lead to the conclusion that cortical planning was not involved in these saccades, and subcortical processes were controlling the saccades. Thus, specific types of presaccadic ERP activity should occur in relation to saccades when visual expectations about the occurrence of the upcoming stimulus location have been made or if the infant is expecting a target in a specific location based on the existence of the peripheral cue. Alternatively, irregular sequences that do not result in saccadic anticipation may not have presaccadic ERP changes.

The existence of the presaccadic ERP changes is not unequivocal evidence for cortical areas involved in saccade planning. It is possible that cortical activity may occur that is involved in other aspects of eye movement or attention shifting (e.g., disengagement of attention in parietal cortex) and is still closely linked to saccades. In addition, cortical activity may be epiphenomenal to the saccadic control that occurs in a subcortical location. Saccade planning in these procedures may be done in different brain areas. For example, it has been hypothesized that the striatum (caudate and putamen of the basal ganglia) controls the anticipatory looking in the visual expectation procedure (Nelson, 1995). Neural activity in this subcortical area may or may not be reflected in EEG activity, which is sensitive to cortical but not subcortical activity. Finally, the lack of presaccadic ERP activity associated with reflexive saccades would be interpreted as the control of these saccades by primarily subcortical eye movement systems (e.g., superior colliculus).

It would be beneficial to follow up these studies with very high-density EEG recording systems (e.g., 64 channel in Csibra et al., 1997; Csibra et al., 1998, this is-

sue; 128 or 256 channel in Tucker, 1993, or Tucker, Liotti, Potts, Russell, & Posner, 1994). Such high-density EEG recording allows the use of cortical dipole localization techniques so that specific locations in the cortex that are known to affect eye movements may be tested as being responsible for the presaccadic ERP changes. Other neuroimaging studies (functional magnetic resonance imaging, positron emission tomography) have been used with adult participants in this type of study, and if they could be used with infant participants they also would be helpful in localizing the cortical areas involved in saccadic planning. These three studies represent an admirable attempt to begin the study of cortical indexes of saccade planning in young infants.

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