OVERLAPPING CORTICAL REGIONS FOR READING AND TEMPORAL PROCESSING IN DEVELOPMENTAL DYSLEXIA

by

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ABSTRACT

Children with developmental dyslexia have difficulty learning to read. These children may also have deficits in temporal processing, which is the perception and integration of rapidly presented stimuli. Behavioural research indicates a link between reading and temporal processing ability; however, the cortical relationship between these two skills has not been established. This thesis examined whether tasks of reading and temporal processing activate similar cortical regions in children with average reading ability and in children with dyslexia. Using functional magnetic resonance imaging (fMRI), activity for two reading tasks (phonological and orthographic) and two temporal processing tasks (dichotic pitch and global motion perception) was assessed. Three regions of interest were established in each participant: the lateral occipital cortex (LOC) and areas engaged by dichotic pitch and global motion tasks. Results demonstrated that both groups had increased activity in bilateral LOC during reading. In average readers, left LOC was more active than right regions during the phonological task, while dyslexic readers showed equivalent activity between left and right LOC for both reading tasks. The dichotic pitch regions did not show any evidence of activation during reading in either group. However, children with dyslexia exhibited significant activity in right global motion regions during the phonological task, but only on the difficult word condition. Average readers did not illustrate activation in global motion areas during reading. The current results suggest that LOC is involved with the reading process and children with dyslexia may have a deficit in left LOC. It was hypothesized that dyslexic readers may have increased attentional processing and recruitment from additional cortical regions during difficult tasks, which may explain the similar activity between global motion and phonological reading. Since there were no similar regions between dichotic pitch and reading, this suggests that these may not be directly related through cortical activity. The current results provide novel evidence that reading and visual temporal processing may involve some of the same cortical areas, at least in children with dyslexia. Future research will investigate links between reading and temporal processing in younger children and will examine differences in white matter connectivity.

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Finally to all of the children, families and schools that have participated in this research. It could not have been possible without you, and I hope that this research will assist children with dyslexia in the future.

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1. INTRODUCTION

Developmental dyslexia is defined as difficulty learning to read, despite average intelligence, motivation, lack of sensory impairments and adequate access to educational resources (Lyon, Shaywitz, & Shaywitz, 2003). This learning disability affects 5 to 17% of school-aged children, and while the etiology is unknown, there may be a genetic or neurobiological basis (Fisher & DeFries, 2002; Habib, 2000; Shaywitz, 1998). Additionally, reading deficits tend to persist into adulthood and they may not disappear even though the child has received remediation (Jacobson, 1999).

It is well established that most persons with dyslexia experience difficulty with phonological encoding and decoding, which includes awareness of letter-to-sound correspondences (Snowling, 1981; Stanovich & Siegel, 1994) and accurate phonological representations of words (Fowler, 1991; Swan & Goswami, 1997). A deficit in learning the phonological rules of language has been suggested as the main cause of dyslexia (Stanovich, 1988). Some dyslexic readers may have deficits in orthographic processing, which includes awareness of irregular words that do not have phonological representations, such as 'yacht' (Castles & Coltheart, 1993).

Children and adults with dyslexia may also have difficulty with temporal processing, which is defined as the perception and integration of rapidly presented stimuli in either vision or hearing (reviewed in Farmer & Klein, 1995). Auditory temporal processing deficits have been shown with increased errors on temporal ordering of tones (Tallal, 1980), auditory gap detection (Farmer & Klein, 1993), frequency modulation (Stein & McAnally, 1995) and dichotic pitch perception (Dougherty, Cynader, Bjornson, Edgell, & Giaschi, 1998; Edwards et al., 2004). Visual temporal processing deficits have been shown with reduced contrast sensitivity for dynamic gratings of low spatial frequency or short stimulus duration (Edwards et al., 2004; Slaghuis & Ryan, 1999), flicker-defined shape perception (Sperling, Lu, Manis, & Seidenberg, 2003), speed discrimination (Demb, Boynton, Best, & Heeger, 1998) and global motion perception (Cornelissen, Richardson, Mason, Fowler, & Stein, 1995; Edwards et al., 2004). It has been postulated that deficits in temporal processing may cause the reading problems shown in dyslexia (Farmer & Klein, 1995; Tallal, 1980); however, this relationship between reading and temporal processing remains controversial.

Functional neuroimaging has shown that average readers engage three primary left hemisphere regions during reading, including the inferior frontal gyrus, parietal-temporal and occipital-temporal regions (reviewed in Shaywitz, Lyon, & Shaywitz, 2006). Dyslexic readers may have a disruption in parietal-temporal and occipital-temporal regions, as illustrated by decreased cortical activity within these areas in comparison to average readers (Horwitz, Rumsey, & Donohue, 1998; Shaywitz et al., 2002; Temple et al., 2001). Similarly, persons with dyslexia may have decreased activity in the middle temporal (MT) cortex during tasks of visual temporal processing (Demb, Boynton, & Heeger, 1997, 1998; Eden et al., 1996) and decreased activity in left superior and middle frontal gyri during an auditory temporal processing task, relative to average readers (Temple et al., 2000). These results suggest that children and adults with dyslexia have decreased activation in cortical regions that are utilized for both reading and temporal processing.

There is evidence to suggest a behavioural link between temporal processing and reading ability (reviewed in Farmer & Klein, 1995). Results from functional neuroimaging have shown that reading and temporal processing may activate some of the same cortical regions, such as the occipital-temporal cortex. However this cortical relationship has not been established empirically. If tasks of reading and temporal processing activate similar regions, this may provide additional evidence for the role of temporal processing in reading ability and disability, as well as further our understanding of the neural deficits underlying dyslexia. ***The main objective of this thesis was to determine if the regions activated by temporal processing are also activated by reading in children with average reading ability and in children with dyslexia.***

1.1. Theories of developmental dyslexia

Three principal theories have emerged for the basis of developmental dyslexia. These have focused on phonological processing, the cerebellar system and the magnocellular system (reviewed in Ramus et al., 2003). There are separate proposed deficits and neural mechanisms underlying each theory.

In the phonological processing theory, learning the letter-to-sound correspondences in a language has been hypothesized as the basis of learning to read (Stanovich, 1988). Phonological skills are typically measured by the ability to read non-words (e.g., 'clabom').

There is ample evidence showing that children with dyslexia have increased errors in reading non-words in comparison to age-matched average readers (Siegel & Ryan, 1988; Snowling, 1981; Waters, Bruck, & Seidenberg, 1985). It has also been suggested that poor performance on phonological tasks may not be the result of deficient phonological analysis skills, but rather results from inaccurate phonological representations of words (Fowler, 1991; Hulme & Snowling, 1992). Decreased cortical activity in the left Sylvian region (Paulesu et al., 1996, 2001; Pugh et al., 2000; Shaywitz, 1998; Shaywitz et al., 2002; Temple et al., 2001) and bilateral MT (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2007), as well as decreased white matter integrity in the left parietal-temporal cortex (Klingberg et al., 2000) have been associated with poor phonological skills. These results suggest that multiple cortical regions are utilized for phonological processing; however the precise neural mechanism remains unknown. Most researchers do not dispute the existence of a phonological deficit in dyslexia, but it may be only one aspect of a more general disorder.

The second theory of dyslexia, which involves the cerebellar system, postulates that impairments in the cerebellum are manifested as deficits in balance and the automatization of skills (Fawcett, Nicolson, & Dean, 1996; Nicolson & Fawcett, 1990, 1994). Persons with dyslexia have shown deficits in motor functioning (Fawcett et al., 1996), automatizing balance (Nicolson & Fawcett, 1990) and rapid automatized naming of objects, colours, numbers and letters (reviewed in Denckla & Cutting, 1999). Thus, it has been suggested that a cerebellar dysfunction may play a role in dyslexia via routes that affect writing, reading and spelling (Nicolson et al., 1999; Nicolson, Fawcett, & Dean, 2001). For instance, abnormal cerebellar function results in decreased motor skills, which may lead to decreased writing ability. Another route suggests that mild motor problems in the infant are exacerbated and are manifested as articulation difficulties when learning to speak. These articulation difficulties impair the ability to learn the phonemic structure of language and therefore, also impair reading acquisition. Finally, deficits in automatizing skills may affect the capacity to learn proper spelling of words, which may explain the poor spelling skills in dyslexia. Through neuroimaging, it has been shown that dyslexic readers have anatomic, metabolic and activation abnormalities in the right cerebellum, in comparison to average readers (Leonard et al., 2001; Nicolson et al., 1999; Rae et al., 1998). These results suggest that the

cerebellum is one mechanism that may be affected in dyslexia, as shown by both behavioural and neural deficits.

The final hypothesis proposes that the magnocellular (M) visual system is impaired in dyslexia (Stein & Walsh, 1997). In contrast, the parvocellular (P) pathway remains intact and is not affected. This subcortical hypothesis has remained controversial, however, the dorsal projections from the M pathway may affect abilities such as visual temporal processing and aspects of visual attention (reviewed in Boden & Giaschi, 2007). Children and adults with dyslexia may have difficulty in shifting and disengaging attention (Hari & Renvall, 2001; Partanen, Prevost, von Grünau, & Giaschi, submitted b), in covert tasks or when attending to space without moving the eyes (Buchholz & Davies, 2005; Heiervang & Hugdahl, 2003), as well as in visual search tasks such that they search less efficiently for targets amongst distractors (Buchholz & McKone, 2004; Ruddock, 1991). Reading may benefit from an increased attentional focus; for instance, an attentional spotlight may be deployed during each fixation and this may assist in the spatial and temporal attentional shifts that occur during reading (Vidyasagar, 1999). If children have deficits with shifting and maintaining attention to an object in space, they may also have problems with attending to letters in words. Additionally, persons with dyslexia may have difficulty with temporal processing; a deficit in perceiving rapidly presented stimuli, such as the letters and sounds of words, may slow the acquisition of reading (Farmer & Klein, 1995; Tallal, 1980). Temporal processing deficits are discussed further in subsequent sections.

The M visual pathway includes subcortical projections from the retina to V1 via the lateral geniculate nucleus (LGN), which then proceeds to cortical areas such as MT and posterior parietal cortex through the dorsal pathway. It has been shown that dyslexic readers have smaller cell bodies in the M layers of the LGN (Livingstone, Rosen, Drislane, & Galaburda, 1991) and decreased cortical activity in MT, but not V1, during a coherent motion task (Eden et al., 1996). During a visual attention task, adults with dyslexia showed decreased activity in left superior and inferior parietal regions in comparison to average readers (Peyrin et al., 2009). Further evidence of M/dorsal pathway involvement is supported by studies using transcranial magnetic stimulation, which found that reading accuracies decreased after stimulation of MT (Laycock, Crewther, Fitzgerald, & Crewther, 2009) and reading reaction times were slowed after stimulation of the right parietal cortex

(Braet & Humphreys, 2006). These results suggest that the M/dorsal visual pathway is affected in dyslexia; however other researchers have failed to find a specific M pathway deficit (Amitay, Ben-Yehudah, Banai, & Ahissar, 2002; Ben-Yehudah, Sackett, Malchi-Ginzberg, & Ahissar, 2001; Williams, Stuart, Castles, & McAnally, 2003).

A generalization of this hypothesis postulates that the M dysfunction is not restricted to the visual pathways, but can influence the auditory and tactile modalities as well (Stein, 2001). In the auditory system, there is no distinct M pathway from subcortical to cortical regions. However, there are large M-type neurons that relay signals to the auditory cortex, which are able to track the frequency and amplitude changes of phonemes (Trussell, 1999). Others have demonstrated that M cells of the medial geniculate nucleus (MGN) in dyslexic readers were disordered and smaller than in average readers (Galaburda, Menard, & Rosen, 1994). Psychophysical evidence has shown that persons with dyslexia needed greater changes in frequency or amplitude to distinguish between two tones (McAnally & Stein, 1996; Talcott et al., 1999; Witton, Richardson, Griffiths, Rees, & Green, 1997). This was suggested as evidence that the M auditory system is also impaired in dyslexia.

Three major theories have attempted to explain the basis of reading deficits; however the precise neural mechanism underlying dyslexia remains unknown. ***This thesis did not employ a specific theory of dyslexia, but rather the neural correlates of reading and temporal processing deficits were investigated.***

1.2. Component reading ability

Normal reading development in children has been hypothesized to include three stages (Frith, 1985). In the first stage, children recognize words by distinct visual properties or the morphological structure within words, such as double 't' in 'bottle'. This stage is followed by learning that letters are associated with sounds, or a grapheme-to-phoneme correspondence. Finally, children proceed to utilizing orthographic information to recognize words, which is akin to developing a mental dictionary of words. In average reading children, it has been shown that an early reliance on phonology proceeds to orthography with experience, as shown in reading aloud (Backman, Bruck, Hebert, & Seidenberg, 1984; Waters, Seidenberg, & Bruck, 1984) and in silent reading (Coltheart, Laxon, Rickard, & Elton, 1988; Johnston, Thompson, Fletcher-Flinn, & Holligan, 1995).

In skilled readers, the process of reading aloud has been modeled using a dual route cascade, which involves both phonological and orthographic components (Coltheart, Curtis, Atkins, & Haller, 1993). In the phonological or non-lexical route, letters are associated with phonemes and this allows a person to read non-words correctly (e.g. 'trope'). In the orthographic or lexical route, a mental dictionary of words is developed, which allows a person to read irregular words (e.g. 'gauge'). Skilled readers are able to use both of these routes in order to read aloud accurately.

The distinction between phonological and orthographic reading was first demonstrated in patients with left hemisphere brain damage. Deep, or dysphonetic, dyslexia is defined as deficits in non-word reading but adequate performance in irregular word reading; these patients had damage in the left Sylvian fissure (Coltheart, Marshall, & Patterson, 1986; Marshall & Newcombe, 1966). Poor non-word reading in these patients was an indication that the phonological processing system was damaged. Surface, or dyseidetic, dyslexia is manifested by deficits in irregular word reading but adequate performance in non-word reading; these patients had damage in the left parietal-temporal region (Marshall & Newcombe, 1973; Shallice, 1981). Poor irregular word reading was an indication of damage to the orthographic processing system.

Developmental dyslexia, on the other hand, is not characterized by acquired reading deficits but rather by deficits in the acquisition of reading. Children with dyslexia have shown deficits on phonological reading tasks (Snowling, 1981; Stanovich & Siegel, 1994) and some evidence suggests that these children may also have deficits in orthographic processing (Castles & Coltheart, 1993). Dyslexic readers may have problems in either phonological or orthographic processing, or a combination of both (Boder, 1973; Castles & Coltheart, 1993). These results were used as evidence that phonological and orthographic processing are separate components of reading. ***This thesis utilized tasks of phonological and orthographic reading in order to determine whether children with dyslexia in the current sample were impaired on one or both processes.***

1.3.   Auditory and visual temporal processing deficits

Children and adults with dyslexia have shown deficits in auditory and visual temporal processing, as demonstrated by various tasks and researchers (reviewed in Farmer & Klein,

1995). In auditory temporal order judgement, the task is to determine the order of tones that are separated by varying inter-stimulus intervals (ISI). Persons with dyslexia demonstrated more errors on sequencing tasks than average readers, especially at shorter ISIs (Ben-Artzi, Fostick, & Babkoff, 2005; Cestnick & Jerger, 2000; Farmer & Klein, 1993; Tallal, 1980). Gap detection is a task based on the presentation of non-speech tones containing silent gaps of differing lengths. Reading impaired populations needed greater gap lengths than average readers to detect a silent break in the tone (Farmer & Klein, 1993; Van Ingelghem et al., 2001). In pure auditory frequency discrimination, adults with dyslexia needed greater changes in frequency to detect a difference in pitch than average readers (McAnally & Stein, 1996). Similarly for frequency modulation detection and discrimination, dyslexic readers were impaired at detecting low frequency modulating tones (Witton et al., 1998) and they needed greater changes in frequency modulation to detect a difference between two tones (Stein & McAnally, 1995). Finally, dichotic pitch is an auditory stimulus created using two sound sources such that the fusing of binaural cues is needed to perceive pitch while monaural cues on their own cannot be used. In this task, sequences of ascending or descending tones are presented within background noise and the task is to indicate the location or direction of pitch. It has been shown that the majority of children with dyslexia do not perceive dichotic pitch, in comparison to age-matched average readers (Dougherty et al., 1998; Edwards et al., 2004).

Persons with dyslexia have also demonstrated visual temporal processing deficits. In spatial frequency perception, sinusoidal gratings over a range of spatial frequencies are presented at various contrast levels; the task is to indicate whether the gratings are visible. Poor readers have lower contrast sensitivity especially at low spatial frequencies and short stimulus durations (Lovegrove et al., 1982; Slaghuis & Ryan, 1999), in addition to needing greater changes in spatial frequency to discriminate between gratings relative to average readers (Amitay et al., 2002). In flicker-defined shape perception, two displays of black and white dots are presented that reverse polarity in each phase. An outline of a specific shape (e.g., circle) can be perceived from the flickering dot pattern. Increasing the rate at which the dots flicker increases the difficulty in this task. The dyslexic reader group had lower speed thresholds than the average reader group, suggesting that they did not perceive shapes at higher flicker speeds (Sperling et al., 2003). In speed perception tasks, drifting sinusoidal

gratings are presented and the task is to determine the interval in which the gratings moved faster. Adults with dyslexia needed larger changes in speed to detect differences between intervals (Amitay et al., 2002; Demb et al., 1998). Finally in global motion perception, displays of coherently moving dots are presented with a percentage of randomly moving dots and the task is to detect or determine the direction of motion for the coherently moving dots. This task becomes more difficult as the ratio of coherent to randomly moving dots is decreased. Dyslexic reader groups have been shown to have poorer sensitivity on motion detection tasks (Cornelissen et al., 1995) and worse direction discrimination particularly at lower dot densities and slower speeds (Edwards et al., 2004; Slaghuis & Ryan, 1999; Talcott, Hansen, Assoku, & Stein, 2000a; Witton et al., 1998).

Studies investigating both auditory and visual temporal processing have identified deficits in both modalities (Amitay et al., 2002; Edwards et al., 2004; Van Ingelghem et al., 2001; Witton et al., 1998), deficits in only auditory tasks (Farmer & Klein, 1993; Heim, Freeman, Eulitz, & Elbert, 2001), or no deficits in either modality (Kronbichler, Hutzler, & Wimmer, 2002). This ambiguity across studies may be the result of differences in the task, sample or the manner in which dyslexia was defined. However, when comparing across temporal processing tasks in both modalities and utilizing stringent criteria to define dyslexia, it was shown that children with dyslexia had deficits on either auditory or visual tasks, but not both (Edwards et al., 2004). The results of this latter study suggest that there may be sub-groups of readers that illustrate only auditory or only visual temporal processing deficits. *In this thesis, auditory and visual temporal processing tasks measuring dichotic pitch and global motion perception, respectively, were utilized. Performance on these tasks has been shown to be effective at differentiating between average and dyslexic readers (Edwards et al., 2004). Behavioural results were used to determine whether children in this unselected sample were impaired in temporal processing.*

1.4. Relationship between temporal processing and component reading

It has been hypothesized that visual and auditory temporal processing abilities can predict orthographic and phonological reading, respectively (Farmer & Klein, 1995). Various researchers have found that average readers and children with dyslexia illustrate distinct relationships between visual temporal processing and orthographic reading, as well

as between auditory temporal processing and phonological reading (Au & Lovegrove, 2001; Booth, Perfetti, MacWhinney, & Hunt, 2000; Coltheart et al., 1988; Cornelissen et al., 1998; Talcott et al., 2000b). Other evidence suggests that both modalities of temporal processing predict component reading skills in children with varying reading abilities (Talcott et al., 2002).

However most research on the relationship between temporal processing and reading skills has been focused on a single modality. Auditory temporal processing skills have been correlated with phonological reading ability (Boets, Wouters, van Wieringen, & Ghesquière, 2006; Stein & McAnally, 1995; Talcott et al., 1999; Tallal, 1980; Witton, Stein, Stoodley, Rosner, & Talcott, 2002) and with orthographic reading ability in children (Talcott et al., 1999). Some evidence has shown that there is no relationship between auditory temporal processing and phonological reading (Heiervang & Hugdahl, 2003). These studies assessed gap and frequency detection, temporal order judgement, as well as frequency modulation detection and discrimination. Similarly, visual temporal processing skills have been shown to be associated with phonological reading ability (Slaghuis & Ryan, 1999; Talcott et al., 1998) and with orthographic reading in children with reading deficits (Sperling et al., 2003). These studies utilized paradigms with spatial frequency detection and discrimination, global motion detection and flicker-defined shape identification.

From the existing literature, it is difficult to determine whether orthographic and phonological reading are related to modality-specific temporal processing ability. There was no consistent relationship between the type of temporal processing task and component reading ability; similarly there was not a consistent relationship for children and adults or for average and dyslexic readers. ***In this thesis, tasks of auditory and visual temporal processing as well as phonological and orthographic reading were utilized to determine whether there were specific relationships between component reading and temporal processing.***

1.5.   Neurobiology of reading

Young children who are learning to read have increased cortical activity in the left parietal-temporal and occipital-temporal cortex during word recognition and phonological reading tasks (Simos et al., 2001). With increasing age and reading ability, children engage

the left inferior frontal gyrus while reading (Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003; see Figure 1). Adults also display significant activity within these regions; however the left inferior frontal gyrus is more strongly activated during reading than in children (Shaywitz et al., 2006; Simos et al., 2001; Turkeltaub et al., 2003). Activity in the left inferior frontal gyrus and occipital-temporal regions has been correlated with greater word reading and phonological awareness skills (Ben-Shachar et al., 2007; Rimrodt et al., 2009; Turkeltaub et al., 2003). These results were taken as evidence that brain systems change according to age and reading skill.

Figure 1. Left hemisphere regions active during reading
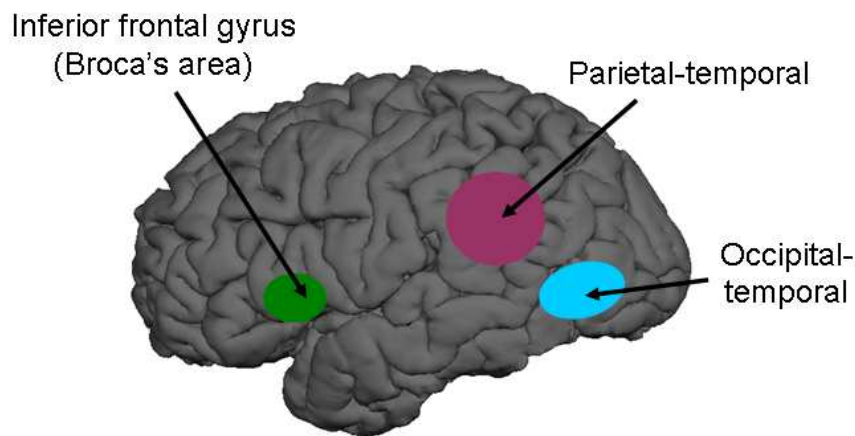
Cortical surface image adapted from control participant C04.

The left lateral posterior hemisphere is disrupted in children with dyslexia, as shown by decreased activity in left parietal-temporal and occipital-temporal regions during reading, in comparison to children with average reading ability (Horwitz et al., 1998; Shaywitz et al., 2002; Temple et al., 2001). Dyslexic readers illustrate increased activation in the right inferior frontal and middle temporal lobes, which is not observed in average readers (Hoeft et al., 2007; Shaywitz et al., 2003). Additionally, persons with dyslexia who have undergone reading remediation demonstrate activation patterns closely resembling those of average readers, with increased activity in the left (Temple et al., 2003) and bilateral inferior frontal

gyri (Richards et al., 2006; Richards & Berninger, 2008), left superior temporal gyrus (Simos et al., 2002) and the left parietal-temporal cortex (Temple et al., 2003). This increase in cortical activation was not shown in dyslexic readers who did not receive remediation or in average readers who received the same treatments. However activity in the right inferior frontal gyrus was still observed in some children with dyslexia before and after remediation. It has been suggested that a disruption in the left lateral posterior cortex may result in increased recruitment from right hemisphere regions. This pattern of activity may assist in compensating for the poor reading skills shown in dyslexia (Shaywitz et al., 2002)

For tasks of component reading, average readers illustrate increased activity in left frontal and temporal regions during phonological reading and increased activity in left fusiform and extrastriate regions during orthographic reading (Booth et al., 2004; Pugh et al., 1996). Other results, however, have indicated that orthography and phonology are processed in similar left frontal and temporal regions (Haist et al., 2001; Rumsey et al., 1997). A meta-analysis has suggested that phonological reading is mediated by left hemisphere regions such as the superior temporal gyrus, supramarginal gyrus and the inferior frontal gyrus, while orthographic reading activates inferior and middle temporal gyri (Jobard, Crivello, & Tzourio-Mazoyer, 2003). It has been shown that children with dyslexia have decreased activity in left parietal-temporal regions for phonological reading and in left occipital-parietal regions for orthographic reading (Temple et al., 2001, 2003). These results suggest that phonological and orthographic reading may be processed in separate cortical systems and that children with dyslexia may have abnormal activity within these regions.

Differences between average and dyslexic reader groups are also evident in studies of brain anatomy. Myelination of the left parietal-temporal cortex has been correlated to increased reading ability (Klingberg et al., 2000; Nagy, Westerberg, & Klingberg, 2004) and participants with dyslexia demonstrated decreased grey matter and white matter fractional anisotropy within this region (Brown et al., 2001; Deutsch et al., 2005). In adults with dyslexia, regions that showed decreased cortical activity, such as the left middle and inferior temporal gyri and left arcuate fasciculus, also showed altered density in grey and white matter (Silani et al., 2005). These findings illustrate that in addition to functional deficits, dyslexic readers may also have neuroanatomical abnormalities in comparison to average readers.

Persons with dyslexia may have a disruption in left lateral posterior regions, as evidenced by both functional and anatomical neuroimaging findings. The cause of this disruption, however, remains unknown. ***This thesis investigated the activation patterns during phonological and orthographic reading in children with average reading ability and in children with dyslexia. A specific examination of anatomical deficits was not conducted.***

1.6.   Neurobiology of temporal processing

Only a few neuroimaging studies have focused on temporal processing and dyslexia. Visual temporal processing tasks assessing speed discrimination and global motion perception activated bilateral MT in average readers (Ben-Shachar et al., 2007; Eden et al., 1996; Giaschi, Zwicker, Au Young, & Bjornson, 2007). More importantly, however, is that phonological awareness in children was correlated to activation in MT, but not V1 (Ben-Shachar et al., 2007). Additional studies with adults with dyslexia demonstrated less activity within MT during a global motion task (Eden et al., 1996) and less activity in both V1 and MT during a speed discrimination task, relative to average readers (Demb et al., 1997, 1998). An auditory temporal processing task with rapidly changing acoustic stimuli activated the left superior and middle frontal gyri for average reading adults, but not for adults with dyslexia (Temple et al., 2000). These results suggest that the behavioural temporal processing deficits shown in dyslexia may also be reflected as functional deficits in brain activity. ***In this thesis, cortical activity for auditory and visual temporal processing was assessed using tasks of dichotic pitch and global motion perception. These tasks were used to identify differences in cortical activity between children with average reading ability and those with dyslexia.***

1.7.   Current project

Previous research has postulated that there is a behavioural link between reading and temporal processing ability (Farmer & Klein, 1995), yet this relationship remains controversial. Neuroimaging evidence suggests that the regions activated by reading tasks are close to the regions activated by temporal processing tasks (Ben-Shachar et al., 2007; Demb et al., 1997, 1998; Eden et al., 1996); however the cortical association between reading and temporal processing has not been established empirically. In order to examine the

cortical relationship between reading and temporal processing, this thesis utilized functional magnetic resonance imaging (fMRI) to address the following objectives.

The main objective was to determine if the regions activated by temporal processing are also activated by reading in children with average reading ability and in children with dyslexia. In average readers, it was hypothesized that reading and temporal processing would activate some of the same cortical regions, such as MT which is known to be activated for a visual temporal processing task of global motion (Eden et al., 1996) and the superior temporal gyrus which is activated for an auditory temporal processing task of dichotic pitch (Giaschi, Bjornson, Dougherty, & Au Young, 2000). Additionally, it was hypothesized that children with dyslexia would have abnormal activity within these regions in comparison to children with average reading ability (Ben-Shachar et al., 2007; Demb et al., 1997, 1998; Eden et al., 1996). If a functional link between reading and temporal processing is apparent in either average or dyslexic reader groups, this would provide further evidence for the role of temporal processing in reading ability.

This thesis also investigated whether a cortical relationship was evident between component reading and temporal processing within specific modalities. Behavioural studies have suggested that auditory and visual temporal processing abilities may demonstrate a relationship with phonological and orthographic reading, respectively (Au & Lovegrove, 2001; Booth et al., 2000; Cornelissen et al., 1998; Talcott et al., 2000b). This behavioural association has not been examined using functional neuroimaging. In this thesis, cortical activation patterns for tasks of auditory and visual temporal processing and tasks of phonological and orthographic reading were examined. It was hypothesized that auditory temporal processing would share some of the same cortical regions as for phonological reading, while visual temporal processing would share some of the same cortical regions as for orthographic reading. If phonological reading / auditory temporal processing or orthographic reading / visual temporal processing activate similar cortical regions, this would provide evidence that component reading and temporal processing mechanisms within each modality are functionally related.

An additional consideration in this thesis was an adjacent region to MT, the lateral occipital cortex (LOC), which is typically utilized for object shape perception (Grill-Spector et al., 1999; Grill-Spector, 2003; Malach et al., 1995; Vinberg & Grill-Spector, 2008). Both

of these regions (MT and LOC) are located in close proximity to regions activated for reading. Thus, this thesis utilized functional localizer tasks for MT and LOC, which would determine if reading activates one or both of these regions. It was hypothesized that LOC would be activated during reading (Grill-Spector, 2003), given that the LOC is utilized for shape perception, it may also be utilized for word form perception. The LOC is anatomically separate from a region located further anterior on the fusiform gyrus, the visual word form area (Cohen et al., 2002). The visual word form area may be utilized solely in reading; it is unknown whether the LOC is also involved with reading.

This thesis is separated into two experiments. The first experiment was used to determine reaction times for reading one or two words on a screen. These reaction times were subsequently utilized for designing the fMRI reading tasks. The second experiment was focused on a) establishing behavioural performance on tasks of reading and temporal processing and b) determining the cortical activation associated with these tasks using fMRI.

2. EXPERIMENT 1

2.1. Introduction

Previous research has indicated that phonological and orthographic processing may be separate components of reading ability (Boder, 1973; Castles & Coltheart, 1993). One goal of this thesis was to determine whether cortical areas involved in component reading ability are related to those involved in auditory and visual temporal processing. A previous fMRI reading paradigm used in our lab demonstrated that the task was too difficult for children with dyslexia, as indicated by their low accuracies while in the scanner. The purpose of the first experiment was to establish whether a new fMRI reading paradigm would be more appropriate for children with dyslexia.

In the previous paradigm, two letter strings were presented on the screen and the child decided which letter string sounded like a real word (phonological condition) or looked like a real word (orthographic condition). These conditions were presented in alternating order within one fMRI run, which likely increased the difficulty of the task. Therefore in the current behavioural experiment, the reaction times and accuracies for a two-word choice (previous paradigm) or a one-word choice condition (new paradigm) were recorded outside the scanner. It was hypothesized that a one-word choice paradigm would have faster reaction times than a two-word choice paradigm. These data were utilized to design tasks for the fMRI experiment (Experiment 2).

2.2. Methods

2.2.1. Participants

There were 13 children with average reading ability (8 male, 5 female) and 12 children with dyslexia (7 male, 5 female) between 11 and 15 years old. Children were placed in their respective reading groups based on performance on the Gray Oral Reading Test, 4th edition (GORT-4) (Wiederholt & Bryant, 2001). Reading fluency was established by the rate and accuracy of reading aloud short paragraphs. Average readers were characterized by a fluency score greater than or equal to 1 *SD* below the standardized norm ($M = 10$, $SD = 3$; i.e., scaled score of 7 or greater) and dyslexic readers were characterized by a fluency score less than or equal to 1.5 *SD* below the standardized norm (i.e., scaled score of 5 or less). None of the participants had scores between these two ranges (i.e., scaled score of 6).

Participants were not included if their history indicated dyslexia but they did not meet this criterion in GORT-4 testing ($n = 4$; not included in previous statistics). Groups were similar in age, but were significantly different on the reading measures (see Table 1). Children were recruited from an existing laboratory database, newspaper and community advertisements and schools specializing in learning difficulties.

Table 1. Mean (and *SD*) for age and reading measures in Experiment 1

Measure	Average readers	Dyslexic readers	t (df = 23)
Age (years) [a]	14.31 (.70)	13.53 (1.40)	1.73
GORT-4 [b]			
Rate	11.62 (2.26)	5.08 (2.71)	6.57 *
Accuracy	10.77 (1.48)	4.75 (2.56)	7.26 *
Fluency	11.54 (2.44)	3.67 (2.54)	7.92 *

[a] Equal variances not assumed; [b] GORT-4 performance is reported as scaled scores ($M = 10$, $SD = 3$); *Groups significantly different, $p < .001$.

2.2.2. Stimuli and apparatus

In the one-word condition, words were presented in the center of the screen. The shortest word (3 letters in length) measured 2.78 x 1.56 deg and the longest word (11 letters in length) measured 10.64 x 1.56 deg. In the two-word condition, the words were presented 1.74 deg below and above fixation. The central fixation dot measured 0.26 deg diameter. Words were the same width and height as for the one-word condition. The words and fixation were black (5.55 cd / m^2) with the remaining background filled with light grey (96.14 cd / m^2; see Figure 2). During practice trials, participants received feedback with a yellow (89.81 cd / m^2) happy face (after a correct response) or sad face (after an incorrect response) presented in the center of the screen (measuring 5.37 deg diameter). Feedback was not provided during the real experimental trials.

Stimuli were presented on a Macintosh G4 computer with a 17" Apple Studio Display monitor with a resolution of 1024 x 768 pixels and a 75 Hz refresh rate. Tasks were programmed in Matlab 5.2 using the Psychophysics Toolbox 2.5 (Brainard, 1997; Pelli, 1997). Behavioural responses for all tasks were made on a MacGravis gamepad. For some

participants, testing was completed at school; in these cases, a Macintosh 17" PowerBook G4 was utilized with the same stimuli and apparatus parameters as above.

Figure 2. Stimuli for Experiment 1
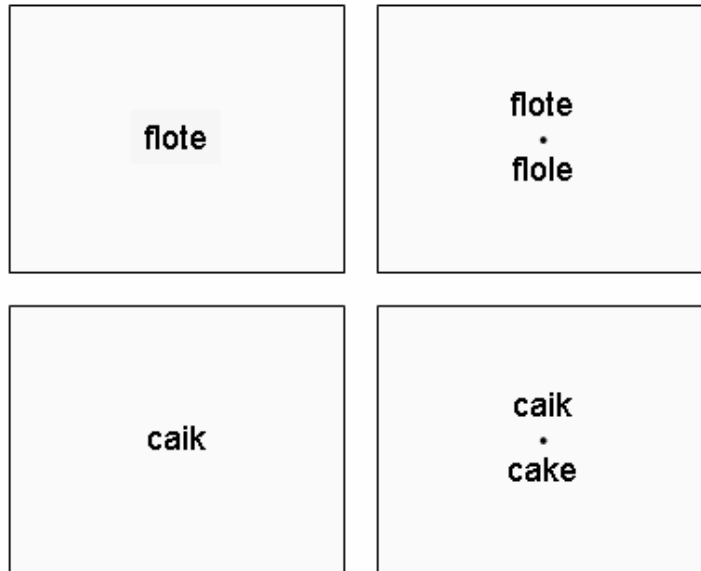
Phonological reading tasks are shown in the top panel. The task was to indicate whether the letter string sounds like a real word (one-word choice, answer is 'yes') or which letter string sounds like a real word (two-word choice, answer is 'top'). Orthographic reading tasks are shown in the bottom panel. The task was to indicate whether the letter string is spelled correctly (one-word choice, answer is 'no') or which letter string is spelled correctly (two-word choice, answer is 'bottom').

2.2.3. Procedure

Participants were seated 66 cm from the computer monitor in a room with photopic lighting. All participants completed 4 reading tasks, which lasted approximately 20 minutes. There were 2 tasks of phonological reading which included one- and two-word choice conditions, and 2 tasks of orthographic reading which also included one- and two-word choice conditions. One-word choice conditions included a presentation of 80 words, while the two-word choice condition included a presentation of 40 word pairs. There were 2 versions of the phonological and orthographic reading lists (see Appendices A and B for all lists). Each participant completed only one version of the reading lists. Words for these tasks were obtained from previous sources (Lukatela & Turvey, 1994; McCann & Besner,

1987; Olson, Kliegl, Davidson, & Foltz, 1984), with the addition of several novel non-words. The order of the 4 tasks was pseudo-randomized for each participant.

Each experiment began with 10 practice trials and the participant proceeded to the test trials if they received at least 70% correct on the practice trials. The one-word choice condition included 80 experimental trials and the two-word choice condition included 40 experimental trials. At the mid-way point of trials, a break was permitted. In phonological reading, the task was to determine whether the letter string sounded like a real word (one-word condition, by indicating 'yes' or 'no') or which letter string sounded like a real word (two-word condition, by indicating 'top' or 'bottom' word). Half of the letter strings sounded like real words; however, none of them were spelled correctly. Therefore in this task, the participant had to rely solely on phonology. For instance, the letter string 'flote' sounds like a real word but is not spelled correctly. There were also non-words included in this condition, such as 'flole' which does not sound like a real word. In orthographic reading, the task was to determine whether the word was spelled correctly (one-word condition, by indicating 'yes' or 'no') or which word was spelled correctly (two-word condition, by indicating 'top' or 'bottom' word). Half of the words were spelled correctly. The incorrectly spelled words were phonetically the same as a correctly spelled word; for instance, the letter string 'caik' sounds like a real word but is not spelled correctly. This design was used to focus on orthography instead of on phonology. The words remained on the screen until the participant provided a response, which was followed by a 200 ms ISI before the next word appeared. Accuracy and reaction times were recorded for each trial.

2.3. Results

The reaction time data were separated into groups of correct and incorrect trials, and were analyzed with a 2 accuracy group (correct, incorrect) x 2 reader group (average, dyslexic) between-within subjects ANOVA. Both one- and two-word conditions were included in these analyses, as this comparison was not of interest at this stage. Degrees of freedom for all error terms were adjusted (Brown & Forsythe, 1974), as the variances between groups were not homogeneous (Levene's test, $p < .15$). For phonological reading, there was no interaction between accuracy and reader groups, $F(1, 362.91) < 1, p > .50$. Reaction times were faster for correct than incorrect trials, $F(1, 398.43) = 24.77, p < .05$, and

average readers showed faster reaction times than dyslexic readers, $F(1, 672.99) = 95.93$, $p < .05$. For orthographic reading, there was a significant interaction between accuracy and reader groups, $F(1, 328.00) = 3.88$, $p < .05$. Simple effect analyses with a Bonferroni correction (to maintain an overall α-level of .05) determined that reaction times were faster for correct than incorrect trials for both average readers, $F(1, 76.49) = 44.17$, $p < .05$, and dyslexic readers, $F(1, 211.89) = 47.71$, $p < .05$. It appeared that the reaction time difference between correct and incorrect trials was larger for the dyslexic reader group than for the average readers (due to the interaction); however this effect was not significant likely due to large variability within the dyslexic group. For both phonological and orthographic reading, results showed that correct trials had faster reaction times than incorrect trials and thus, only correct trials were utilized for subsequent analyses.

In order to determine the effect of one- and two-word conditions, a 2 reader group (average, dyslexic) x 2 condition (one-word, two-word) between-within subjects ANOVA was conducted. The degrees of freedom for the error terms were adjusted with Brown and Forsythe's (1974) procedure because of heterogeneous variances between groups (Levene's test, $p < .15$). For phonological reading, there was a significant interaction between reader group and condition, $F(1, 314.50) = 13.94$, $p < .05$. Simple effect analyses with a Bonferroni correction determined that both average and dyslexic groups obtained faster reaction times for the one-word than the two-word condition [$F(1, 190.27) = 19.81$, $p < .05$; $F(1, 156.99) = 42.73$, $p < .05$, respectively]. It appeared there was a larger difference between one- and two-word conditions for dyslexic readers than for average readers (due to the interaction); however this contrast was not significant likely in response to large variability within the dyslexic reader group. For orthographic reading, there was no interaction between reader group and word condition, $F(1, 245.79) = 2.18$, $p > .05$. Average readers illustrated faster reaction times than dyslexic readers, $F(1, 308.87) = 175.70$, $p < .05$. Also, the one-word condition had faster reaction times than the two-word condition, $F(1, 361.37) = 10.96$, $p < .05$. Figure 3 demonstrates the mean reaction times for correct trials only. Accuracies are listed in Appendix C.

Figure 3. Mean reaction time for one- and two-word reading conditions
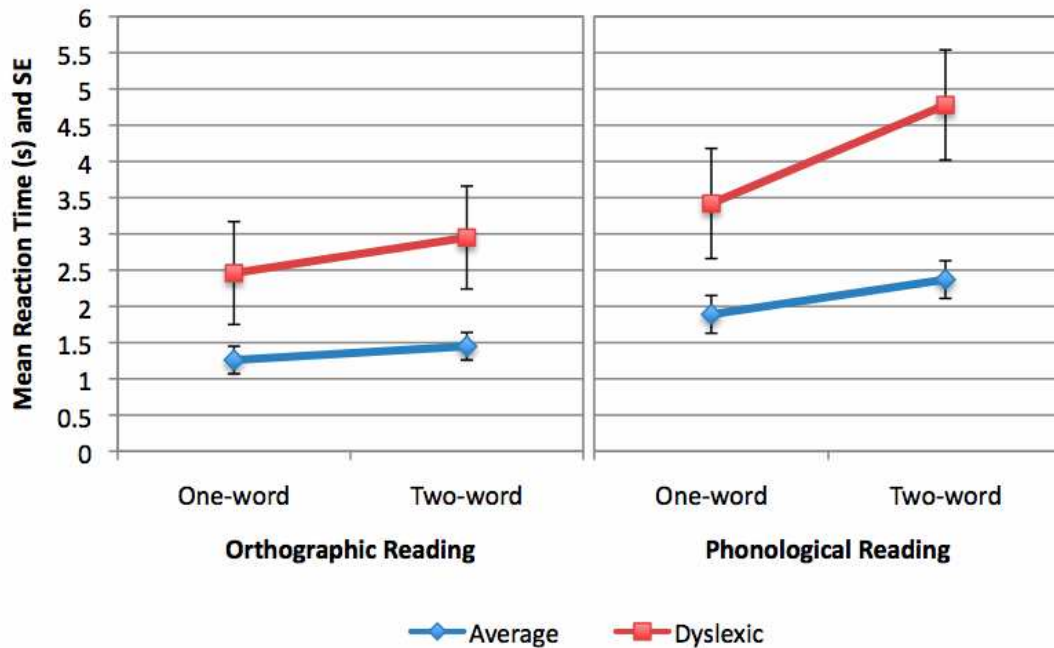
The final analyses determined which variables can predict the reaction time and accuracy of reading phonological and orthographic words. For phonological reading, four variables were included: number of letters in the word (length), word frequency (Harris & Jacobson, 1982), grade-level (Harris & Jacobson, 1982), and similarity to the correctly spelled word. This orthographic similarity was defined as the number of letters by which the phonological word differed from the correctly-spelled version. For example, the phonological word 'beaf' has one letter different than the correctly-spelled word 'beef'. For orthographic reading, 3 variables were included: word length, frequency and grade-level. These variables were then utilized to create novel word lists for the fMRI reading tasks.

Linear regressions were conducted with reaction time and accuracy as dependent variables, and average and dyslexic reader groups were analyzed separately. The predictors were entered as subsequent steps in the regression. The first analyses were completed on the phonological reading task. In the average reader group, none of the variables were significant in predicting reaction times. However, in predicting accuracy, 5% of the variability was accounted for by grade level [F change $(1, 76) = 3.97$, $p < .05$] and 4% of the variability by similarity to the correctly spelled word [F change $(1, 75) = 3.72$, $p < .05$]. For

the dyslexic reader group, 12% of the variability in reaction times were predicted by similarity to the correctly spelled word [F change $(1, 75) = 11.22$, $p < .05$]. Similar results were found with predicting accuracy.

The second set of analyses was completed on the orthographic reading task with reaction times for the average reader group. It was shown that word length predicted 16% of variability in reaction times [F change $(1, 156) = 28.63$, $p < .05$] and grade level predicted 3% [F change $(1, 154) = 5.63$, $p < .05$]. The same variables were significant predictors of accuracy. For the dyslexic reader group, word length predicted 29% of the variability in reaction times [F change $(1, 156) = 64.75$, $p < .05$] and grade level predicted 4% [F change $(1, 154) = 8.73$, $p < .05$]. Similar results were also shown for predicting accuracy. Word frequency was not a significant predictor in either reading groups or conditions. The standardized β coefficients for all predictors and reading tasks are shown in Appendix D.

2.4.   Discussion

The first experiment was designed to determine whether a novel one-word choice reading paradigm would be an improvement over a previous two-word choice paradigm. It was shown that the one-word paradigm had faster reaction times than the two-word paradigm for both average and dyslexic reader groups. Faster reaction and processing times are important for designing fMRI tasks, especially for those with reading difficulties. Since the fMRI task presents a stimulus for a pre-determined amount of time (e.g., 3 s), it would be beneficial to have a task that both reading groups could complete within this period. Therefore, the one-word choice paradigm was utilized for the fMRI experiment (Experiment 2).

Additional analyses demonstrated that the best predictors of orthographic reading were word length and grade level, while for phonological reading the best predictor was similarity to the correctly-spelled word. These predictors were utilized to make word lists for Experiment 2. Word frequency was not a significant predictor of phonological or orthographic reading, which contradicts previous findings by Bruck (1988). However in Bruck's study, the participants were younger than those in the current experiment. It is possible that word frequency may only be a significant factor of reading in younger children; however, adults have also shown an effect of word frequency on reading speed (Balota &

Chumbley, 1984; Whaley, 1978). Another explanation may result from the variability of word frequencies. The current study did not include very low frequency words, while they were utilized in Bruck's study. Further research with a larger word frequency range may determine that frequency is a significant predictor of phonological or orthographic reading speed and accuracy.

Word lists were prepared for the fMRI phonological and orthographic reading tasks based on the findings from Experiment 1 (see Appendices E and F). Average and dyslexic reader groups received different word lists to ensure equivalent accuracy and level of difficulty across groups and therefore, differences in cortical activity between groups would not be attributed to differences in accuracy. The reading tasks were additionally designed to include word lists for easy and difficult conditions for each reading group. For instance in phonological reading, the dyslexic reader group had word lists with one letter different from the correctly spelled word (easy condition) and two letters different (difficult condition), while the average reader group had two letters different (easy condition) and three letters different (difficult condition). For the orthographic reading task, word lists were assembled from Harris and Jacobson's (1982) grade-level lists. The dyslexic reader group received words from primary-level and grades 1 and 2 (easy condition) and grades 2, 3 and 4 (difficult condition), while the average reader group received words from grades 2, 3 and 4 (easy condition) and grades 4, 5 and 6 (difficult condition). The same word lengths were utilized between phonological and orthographic reading tasks. In-scanner accuracies from Experiment 2 determined whether groups had similar performance for the reading tasks, and also whether accuracy varied for the easy and difficult conditions.

3. EXPERIMENT 2

3.1. Introduction

Behavioural research has shown that in addition to poor reading skills, some persons with dyslexia have poorer temporal processing ability than age-matched average readers (reviewed in Farmer & Klein, 1995). However, the role of temporal processing in reading ability remains controversial. Some have postulated that there is a modality-specific relationship between reading and temporal processing. For instance, phonological reading and auditory temporal processing ability, as well as orthographic reading and visual temporal processing ability may be related (Au & Lovegrove, 2001; Booth et al., 2000; Talcott et al., 2000b). The relationships between reading and temporal processing have not been examined empirically using cortical activity.

The main objective of this experiment was to determine if the regions activated by temporal processing are also activated by reading in children with average reading ability and in children with dyslexia. It was hypothesized that temporal processing tasks would engage some of the same regions activated by reading, such as the occipital-temporal cortex (Eden et al., 1996). Furthermore, it was hypothesized that children with dyslexia would have decreased activity in these regions in comparison to average readers (Demb et al., 1997, 1998; Eden et al., 1996; Temple et al., 2000).

An additional investigation was to determine whether there was a cortical relationship between component reading and visual or auditory temporal processing. It was hypothesized that visual temporal processing would share some of the same cortical regions as orthographic reading, while auditory temporal processing would share some of the same cortical regions as phonological reading (Talcott et al., 2000b).

Behavioural performance for component reading and temporal processing was also measured in this experiment. I hypothesized that phonological and orthographic reading as well as auditory and visual temporal processing abilities would be worse for children with dyslexia than for average readers (Castles & Coltheart, 1993; Edwards et al., 2004). Additionally, I hypothesized that auditory temporal processing ability would predict performance on phonological reading, while visual temporal processing ability would predict performance on orthographic reading (Talcott et al., 2000b).

Finally, fMRI tasks were designed with two difficulty levels, which would illustrate whether differences in task performance or the extent of cortical activation were associated with task difficulty. This variation was also included to facilitate comparisons between the average and dyslexic reader groups. For instance, activation differences between groups may be only visible on difficult conditions, but not on easy conditions (Cao, Bitan, Chou, Burman, & Booth, 2006). In-scanner accuracies and cortical activity were measured for easy, difficult and random conditions in reading and temporal processing tasks. It was hypothesized that difficult conditions would demonstrate lower accuracies and higher cortical activity than for easy or random conditions (Kronbichler et al., 2004).

3.2. Methods

3.2.1. Participants

There were 9 children with average reading ability (4 female, 5 male) and 4 children with dyslexia (2 female, 2 male) between 13 and 16 years old. All children were right-handed and were included based on their IQ and reading scores. Each child had at least average intelligence, which was defined as a mean IQ score greater than or equal to 1 *SD* below the standardized norm on the Wechsler Intelligence Scale for Children-IV (WISC-IV) ($M = 10$, $SD = 3$; i.e., all children had scaled scores greater than 7; Canadian norms, Wechsler, 2003). The average IQ score was derived from the block design and vocabulary subtests, which measured performance and verbal IQ, respectively. Assignment to average or dyslexic reading groups was defined according to GORT-4 reading fluency, as described in Experiment 1. One child in the dyslexic reader group scored in the borderline dyslexic reading range; however he demonstrated a history of reading problems as indicated by psychologist and parental reports. Groups were similar on age and IQ measures, while there were significant differences between groups on the GORT-4 reading measures (see Table 2).

Most participants were recruited from Experiment 1 as well as from newspaper advertisements. All participants had normal or corrected-to-normal vision with a decimal visual acuity greater than 0.8 in each eye, which was assessed using the Regan high contrast letter chart (Regan, 1988). All participants also had normal hearing with a threshold of 22.5 dB HL or less in both ears at 500 and 1000 Hz, which was assessed using a Maico MA-39 audiometer.

Table 2. Mean (and *SD*) for age, IQ and reading measures in Experiment 2

Measure	*Average readers*	*Dyslexic readers*	*t (df = 11)*
Age (years)	15.15 (.81)	15.02 (1.28)	.23
WISC-IV [a]			
Verbal IQ (Vocabulary) [b]	11.33 (2.65)	12.50 (4.80)	-.46
Performance IQ (Block Design)	10.89 (2.67)	11.25 (4.65)	-.18
Average IQ [b]	11.11 (2.06)	11.88 (4.48)	-.33
GORT-4 [a]			
Rate	11.67 (2.06)	4.50 (1.29)	6.33 *
Accuracy	11.11 (1.69)	5.00 (2.94)	4.82 *
Fluency	11.89 (2.62)	3.25 (2.63)	5.48 *

[a] WISC-IV and GORT-4 are reported as scaled scores ($M = 10$, $SD = 3$); [b] Equal variances not assumed; *Groups significantly different, $p < .001$.

3.2.2. Behavioural data

3.2.2.1. Apparatus and procedure

Auditory and visual temporal processing tasks were presented on the same apparatus as described in Experiment 1. Participants were seated 74 cm from the computer monitor and the auditory stimuli were presented through Sennheiser HD-265 headphones.

All participants completed reading, IQ and temporal processing measures in the laboratory in one 2-hour session. After informed consent was obtained, the testing session began and the order of the tasks was randomized across participants. Performance on the reading and IQ tasks determined whether the participant was eligible for the fMRI phase, and they were invited to participate after the behavioural testing was completed. Participants were not invited for the fMRI experiment if they had non-removable metal ($n = 2$), were left-handed ($n = 2$), or were not classified as average or dyslexic readers ($n = 4$). These participants were not included in the previous statistics, as shown in Table 2.

3.2.2.2. Reading measures

A modified version of the Coltheart and Leahy (1996) reading lists was used to assess phonological and orthographic reading ability. Participants were asked to read aloud single words and non-words, which were printed on cards and placed in random order in a book (Partanen, Field, & Giaschi, submitted a). There were 30 words in each of three lists: regular

words (e.g., plant), pronounceable non-words (e.g., trope) and irregular words (e.g., yacht). Non-words were used as a measure of phonological reading ability and irregular words were used as a measure of orthographic reading ability. Each participant read the words in the same order at their own pace and the number of errors was recorded.

3.2.2.3.   Temporal processing measures

After receiving instructions for each task, participants completed 10 practice trials at the easiest stimulus level. If participants obtained at least 80% accuracy on this practice, they continued to 20 practice trials using a staircase procedure (described below). All participants demonstrated sufficient accuracy on the practice trials to proceed to the real experimental trials.

Both temporal processing measures utilized a 2-alternative forced-choice procedure with an adaptive two-down, one-up staircase method. The stimulus level decreased (increased difficulty) with two successive correct answers and increased with one incorrect answer. Levels were halved after each response reversal, which is when a response changed from correct to incorrect or from incorrect to correct. The staircase continued until 50 trials were completed or 10 reversals had occurred. Thresholds were determined by fitting a Weibull function to the data using a maximum-likelihood minimization procedure (Watson, 1979). Threshold was defined as the point of maximum slope on the fitted curve, which occurs at 82% correct in a 2-alternative forced-choice procedure (Strasburger, 2001).

Dichotic pitch

Auditory temporal processing was assessed with a dichotic pitch task (Dougherty et al., 1998). This task has been previously shown to differentiate between average and dyslexic readers (Dougherty et al., 1998; Edwards et al., 2004). Dichotic pitch stimuli were generated by filtering two independent, flat-amplitude noise sources. One source was band-pass filtered to create the signal tones, while the other source was notch filtered to create the background noise. The signal and noise were then combined with a time delay, which created the perception of tones that appeared to come from the middle of the head and were embedded in background noise. The complementary signal and noise were modified to adjust the signal-to-background ratio (SBR) from 0 (no signal present; only background noise)

to 1 (equal signal and noise amplitudes) and greater than 1 (signal amplitude higher than noise). At SBR levels less than 1, the tones can only be perceived by fusing the sounds from each ear together using binaural cues. At SBR levels greater than 1, the tones can be perceived at each ear alone. Four tones lasting 200 ms each (400, 575, 750, 900 Hz) were presented in either ascending or descending temporal order.

The task began at SBR 10, with only tones being perceptible at this stage. Participants were asked to determine the direction of pitch of these tones, by indicating 'up' or 'down' on a response pad. The coherence level was initially decreased by two SBR levels and followed the staircase procedure described above.

Global motion

Visual temporal processing was assessed with a global motion task, which has been previously shown to be effective for differentiating between average and dyslexic readers (Edwards et al., 2004). The global motion stimulus was a dynamic random-dot display, which consisted of a percentage of dots moving coherently together in the same direction. The remaining noise dots moved in random directions but at the same speed as the signal dots. The display subtended 23.4 deg horizontally and 18.3 deg vertically and was comprised of white dots (91 cd / m^2) on a black background (0.04 cd / m^2). Dot parameters included a density of 1.0 dots / deg^2, dot size of 0.1 deg diameter and a dot speed of 1.0 deg / s. Each dot had a limited lifetime of 2 frames in the motion movie. This ensured that the participant was not able to follow the path of one dot to determine the direction of motion. The stimuli were displayed for 8 frames of 53.5 ms each, for a total of 427 ms per trial.

The task began at 100% coherence, with all the dots moving in the same direction. Participants were asked to determine the direction of coherent motion by indicating 'left' or 'right' on a response pad. The coherence level was decreased to 80% initially (with 20% noise dots introduced), with subsequent levels adjusted according to the staircase procedure described above.

3.2.3. Functional MRI data

3.2.3.1. Data acquisition and procedure

One week prior to the MRI session, each participant completed a session in a mock MRI scanner at B.C.'s Children's Hospital for approximately 45 min. This allowed participants to practice the tasks and become comfortable with the scanner. They also completed one MRI scanning session at the UBC High Field MRI Centre which lasted approximately 1 hr. A Philips Gyroscan Intera 3.0 Tesla MRI scanner was utilized with an 8-channel phased array head coil (SENSE). A high-resolution T1-weighted 3-D anatomic scan was acquired first and lasted 6 min 34 s. Images were acquired in 170 axial slices (field-of-view, FOV: 256 mm; 256 x 256 mm matrix; TR: 8.0 ms; TE: 3.7 ms; flip angle: 8 deg; 1 mm slice thickness; 1 mm^3 voxel size).

T2*-weighted scans using an echo-planar imaging (EPI) sequence were acquired for the functional data (TR: 2000 ms; TE: 30 ms). For the dichotic pitch scan, a sparse sampling method was used with an effective TR of 2020 ms (actual TR: 7000 ms; TE: 30 ms). All images were acquired in 36 interleaved axial slices (FOV: 240 mm; 80 x 80 mm matrix; flip angle: 90 deg; 3 mm slice thickness; 1 mm inter-slice gap). Images were reconstructed with an 80 x 80 mm matrix, which produced 3 mm^3 isotropic voxels. Tasks varied in duration such that phonological and orthographic reading tasks acquired 168 dynamics (images per slice), global motion acquired 175 dynamics, dichotic pitch acquired 61 dynamics, and the MT and lateral occipital cortex localizers acquired 84 dynamics each.

The stimuli were back-projected with a Panasonic LCD projector with a resolution of 832×624 pixels and refresh rate of 60 Hz. The image was formed on a screen that was 53 cm behind the participant's head and viewed through a mirror that was 15 cm from the participant's eyes. The screen size was 25.4 x 19.4 deg with a projected pixel size of 0.03 deg. Participant responses were obtained using a fiber optic response system (Lumitouch). Each participant wore headphones (Avotec) and earplugs, as well as their head was partially immobilized using head and chin straps.

3.2.3.2. Tasks

All fMRI tasks were programmed in Matlab 7.3.0 using the Psychophysics Toolbox 3.0.8 (Brainard, 1997; Pelli, 1997). The reading and temporal processing tasks were

designed with a parametric variation, which would determine the cortical regions that are modulated by task difficulty. As described below, these tasks included easy, difficult and random conditions. Difficulty levels for: the reading tasks were determined from Experiment 1, the dichotic pitch task from Dougherty et al. (1998) and the global motion task from Edwards et al. (2004).

Phonological and orthographic reading

Phonological and orthographic reading tasks were separate runs in the fMRI protocol, but utilized the same block design. There were 4 conditions which consisted of easy words, difficult words, false font symbols (random) and a fixation cross (baseline). Each 14 s block included 4 trials; the stimuli were presented for 2.8 s with a 700 ms ISI between trials. During the baseline condition, a central cross was presented for 14 s. The 4 blocks were presented in random order within a cycle and each cycle was repeated 6 times, for a total of 24 presentation blocks (336 s). Words and false font symbols were 4 to 6 characters in length, which was equivalent to 1.58 to 3.07 deg wide x 1.3 deg high, displaced 0.31 deg below a fixation cross (see Figure 4 for an example of the phonological reading task). The average and dyslexic reader groups received separate word lists (see Appendices E and F).

For phonological reading, the task was to determine whether the letter string sounded like a real word by indicating 'yes' or 'no' on a response pad. For orthographic reading, the task was to determine whether the letter string was spelled correctly by indicating 'yes' or 'no.' During the false font condition, the participant was asked to respond 'no', and during the fixation cross condition, they were asked to randomly press either button. Time to make a response (reaction time) as well as response accuracy was recorded for each trial.

Figure 4. Stimuli for fMRI phonological reading task
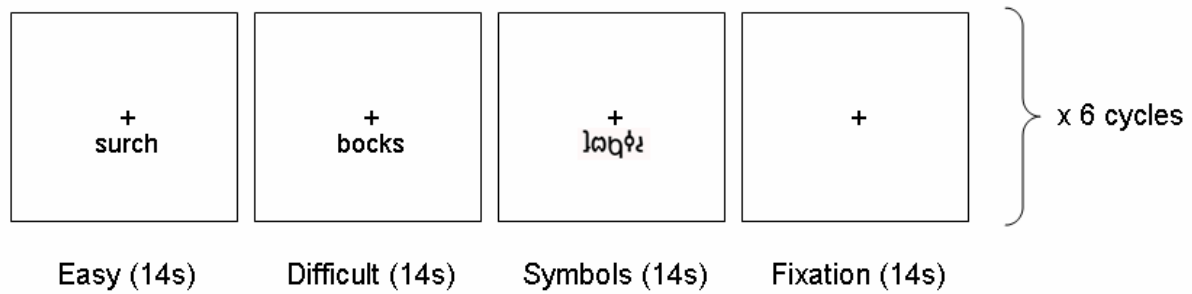
The task was to indicate whether the letter string sounds like a real word (for both easy and difficult conditions, answer is 'yes'). For the symbols condition, the participant was to press 'no', while for the fixation condition, they could press either 'yes' or 'no'.

Dichotic pitch

The dichotic pitch stimulus was presented using an event-related sparse sampling design (Friston, Zarahn, Josephs, Henson, & Dale, 1999; Van den Noort, Specht, Rimol, Ersland, & Hugdahl, 2008). It was determined from pilot testing that participants were unable to hear the auditory stimuli using the regular scanning sequence and thus, the current paradigm utilized sparse sampling. There were 4 conditions which consisted of SBR levels of 10 (easy), 1 (difficult) and 0 (random), as well as a silent period (baseline). Each condition was presented 15 times in random order, for a total of 60 trials (427 s). For each trial, there was a 5 s period during which the stimulus could be played (scanner is quiet) and was followed by a 2 s TR during which images were collected. The stimuli were presented for 1.8 s and the beginning of the sound stimuli were jittered at 1 s, 1.5 s or 2 s after the silent period began. Images were obtained 3 to 6 s after the beginning of the stimulus (see Figure 5). The three jitter times were presented 5 times per condition.

For SBR levels of 10 and 1, a question mark was presented at fixation, which indicated that the participant was to respond during the trial. The task was to determine the direction of pitch by indicating 'up' or 'down' on the response pad. During SBR levels of 0 and the silent period, a central fixation cross was presented. This indicated that the participant did not need to respond during the trial and they were asked to listen to the tones. Accuracy was recorded for SBR levels of 10, 1 and 0. No responses for SBR 0 (accuracy of 0%) was expected for this task.

30

Figure 5. Theoretical BOLD % signal change for fMRI dichotic pitch task
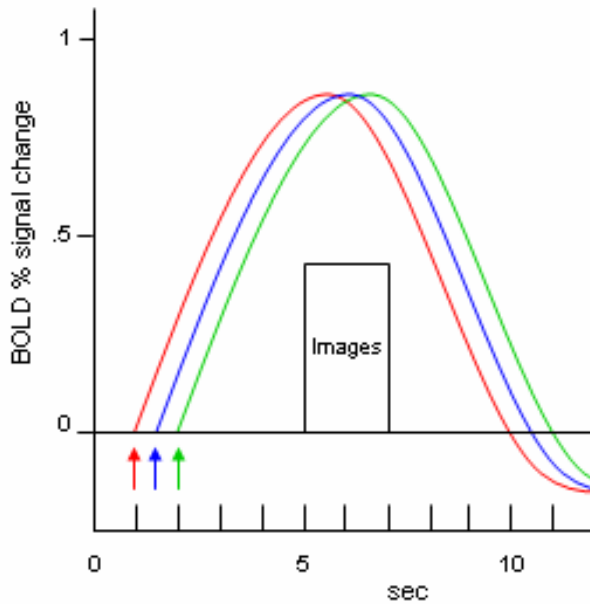
Auditory stimuli were presented for 1.8 s and started at 1 s (red), 1.5 s (blue) or 2 s (green) after the silent period began. Images were collected during 2 s blocks. Theoretical BOLD percent signal functions are shown for each jitter time (BOLD = blood-oxygen-level dependent).
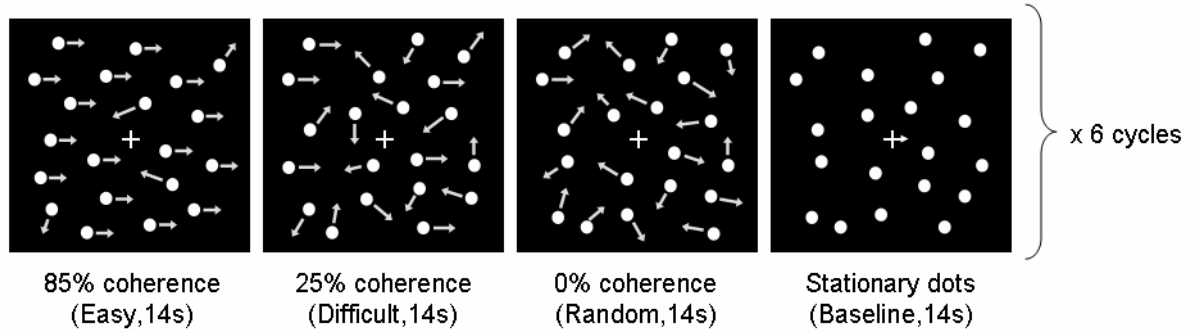
Global motion

The global motion stimulus was similar to that used in the behavioural task described above. There were 4 conditions that consisted of 85% motion coherence (easy), 25% coherence (difficult) and 0% coherence (random), as well as stationary dots (baseline). Each 14 s block included 8 trials; the stimuli were presented for 800 ms with a 950 ms ISI between trials. A cycle began with the stationary dots condition, which was followed by the motion conditions in random order. Each cycle was repeated 6 times and finished with a stationary dots block, for a total of 25 presentation blocks (350 s). Dot parameters included a density of 0.6 dots / deg^2, dot size of 0.1 deg diameter and a dot speed of 0.8 deg / s. A small fixation cross was presented in the center of the screen (see Figure 6).

During the motion conditions, the task was to determine the direction of coherent motion, by indicating 'left' or 'right' on the response pad. For the stationary dots, there was a central arrow presented with the fixation cross and the task was to determine the direction of the arrow, as either 'left' or 'right'. Participants were instructed to maintain fixation and

to not track the moving dots. Accuracy was recorded for each trial. For the 0% coherence condition, 50% accuracy was expected for this task indicating that the participant chose 'left' and 'right' directions equally.

Figure 6. Stimuli for fMRI global motion task

| 85% coherence (Easy,14s) | 25% coherence (Difficult,14s) | 0% coherence (Random,14s) | Stationary dots (Baseline,14s) | } x 6 cycles |

The task was to indicate the direction of the coherently moving dots, as either left or right (in 85% and 25% conditions, answer is 'right', and in 0% condition, answer is either 'left' or 'right'). For the stationary dots condition, the task was to indicate the direction of the central arrow, as either left or right (answer is 'right').

MT localizer

This task was utilized to functionally locate the motion-sensitive area MT, as per previous methods (Giaschi et al., 2007; Huk, Dougherty, & Heeger, 2002; Sunaert, Van Hecke, Marchal, & Orban, 1999; Tootell et al., 1995; Zeki et al., 1991). Blocks of radially moving dots (2.5 deg / s) were alternated with blocks of stationary dots. Each block was presented for 14 s. Within the moving dots condition, 4 trials of expanding dots were alternated with 4 trials of contracting dots, and each trial was presented for 1.75 s. For the stationary condition, dots were presented for a constant 14 s. The cycle of moving dots with stationary dots was repeated for 6 cycles, for a total of 12 presentation blocks (168 s). Grey dots of 0.2 deg diameter with a density of 0.9 dots / deg^2 were presented on a black background for both moving and stationary blocks (see Figure 7). Participants were asked to fixate on a central cross while passively viewing this task.

Figure 7. Stimuli for fMRI MT localizer task

Radially moving dots
(14s)

Stationary dots
(14s)

x 6 cycles
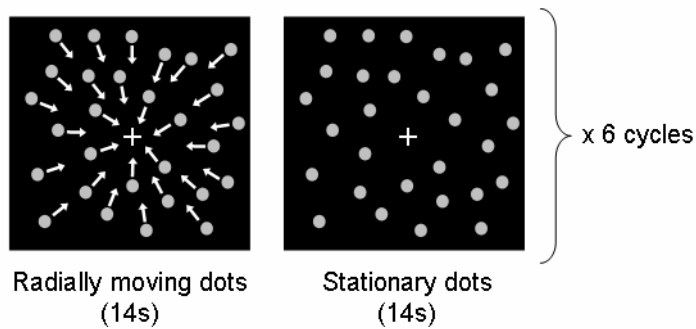
Participants were asked to passively view this task. An example of contracting dots is shown for the radial motion condition, and an example is shown for the stationary dots condition.

LOC localizer

Additionally, there was a functional localizer for the object-sensitive area in the lateral occipital cortex (LOC) (Grill-Spector et al., 1999; Malach et al., 1995). Blocks of coloured object images were alternated with blocks of scrambled object images. Each block was presented for 14 s. Trials consisted of presenting the image for 1 s with a 750 ms ISI between trials. The cycle of unscrambled and scrambled objects was repeated for 6 cycles, for a total of 12 presentation blocks (168 s). All objects were presented at the center of the screen with a fixation cross; images measured 6.04 x 6.04 deg (see Figure 8). Participants were asked to fixate on a central cross and the task was to press the left button if the current picture was the same as the previously presented picture (1-back task). If the pictures were not the same, participants were asked not to respond.

Figure 8. Stimuli for fMRI LOC localizer task

Unscrambled images
(14s)

Scrambled images
(14s)

x 6 cycles
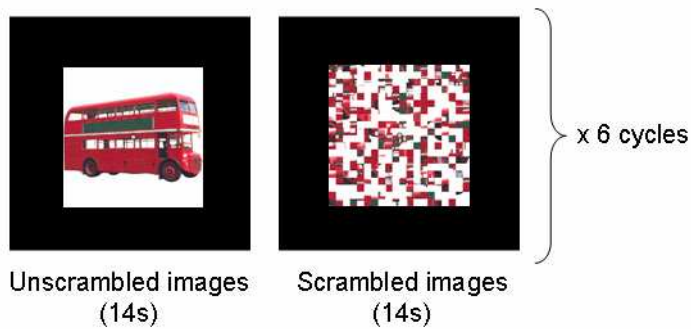
The task was to indicate whether two pictures in a row were the same (for both unscrambled and scrambled conditions). If the pictures were not the same, no response was required.

3.2.3.3.   Pre-processing

BrainVoyager QX 2.0.8 (Brain Innovation, Maastricht, The Netherlands) was used for fMRI analyses (Goebel, Esposito, & Formisano, 2006). Images from the block design sequences (all but dichotic pitch) were pre-processed in 3 separate steps. Slice scan time correction was performed using a cubic spline interpolation, which utilized information from the TR (2000 ms) and the order of image scanning (ascending, interleaved). 3-D motion correction using a six parameter rigid-body tri-linear interpolation was performed to correct for small head movements. All images were aligned to the first image in the time course. Translation (mm) and rotations (deg) were estimated for each time course and images were discarded if these parameters exceeded 3 mm or 3 deg. There were 76 images in total that were deleted from 3 participants (2 average, 1 dyslexic); however, motion was determined to be unrelated to task condition and thus, the remaining data were retained for analyses. Finally, linear trends and non-linear low-frequency drifts of 2 cycles or less were removed with high-pass temporal filtering. For the sparse sampling sequence (dichotic pitch), slice scan time correction and high-pass temporal filtering were not performed as these processes could alter the temporal information necessary for proper data analyses (as per Van den Noort et al., 2008). 3-D motion correction was completed as above. Spatial smoothing using a Gaussian filter (full-width at half-maximum = 4 mm) was applied to these images. The anatomical data for each participant were corrected for intensity inhomogeneities between grey and white matter (Vaughan et al., 2001). The data were interpolated to 1 mm^3 isotropic

voxels and then transformed into standardized stereotaxic atlas space (Talairach & Tournoux, 1988). Functional data were aligned to the standardized anatomical image.

3.2.3.4.   Identification of ROI

After the pre-processing stage, fMRI data were analyzed to determine regions of interest (ROI) for each participant. A single-subjects fixed-effects general linear model (GLM) was utilized to determine whole-brain voxel-wise activity. For the block design scans, predictors were derived by convolution of a box-car waveform with a double-gamma hemodynamic response function (HRF) (Friston et al., 1998). For the event-related scan (dichotic pitch), the predictors did not assume an HRF shape, but rather were defined by the onset of the auditory stimulus. Predictors for phonological and orthographic reading were easy words, difficult words and false font symbols. Dichotic pitch predictors were SBR 10 (easy), SBR 1 (difficult) and SBR 0 (random). Global motion predictors were 85% coherence (easy), 25% (difficult) and 0% (random). The MT localizer predictor was moving dots and the LOC localizer predictor was unscrambled pictures.

Activation maps of the t-statistic were created for each contrast with a Bonferroni-corrected level of $p < .05$ to adjust for multiple comparisons. If a ROI could not be defined with this conservative level of alpha, an uncorrected value of $p < .001$ was used. ROIs were established for MT, LOC, dichotic pitch and global motion tasks. MT was defined as the cluster of contiguous activated voxels in temporal-parietal-occipital cortex, more specifically at the junction between the inferior temporal sulcus and the ascending limb of the inferior temporal sulcus (Dumoulin et al., 2000). LOC was defined as the cluster of activated voxels located posterior to MT along the lateral cortical surface in each hemisphere (Grill-Spector et al., 1999; Malach et al., 1995; Sayres & Grill-Spector, 2008). Regions for dichotic pitch were not determined a priori, but were rather defined as any cluster of activated voxels. Increased activity within bilateral Heschl's gyri, superior temporal sulci and gyri was expected for this task (Giaschi et al., 2000; Puschmann, Uppenkamp, Kollmeier, & Thiel, 2010). The global motion task was expected to activate bilateral MT (Giaschi et al., 2007), intraparietal sulci and superior temporal sulci (Braddick, O'Brien, Wattam-Bell, Atkinson, & Turner, 2000). For all tasks, activity within putative visual areas V1, V2 and V3 were not defined as ROIs, as these were not of interest in this experiment. Finally, for the dichotic

pitch, global motion and LOC localizer tasks, if there were more than one cluster of contiguous voxels activated in each hemisphere, the ROIs were averaged within a hemisphere for analysis purposes.

Six ROIs per participant were utilized for further analyses: bilateral regions for dichotic pitch, global motion and LOC. Regression analyses were conducted to determine whether these ROIs were active during phonological and orthographic reading. These analyses would substantiate whether temporal processing and reading tasks activated the same cortical regions, or whether another adjacent region (such as LOC) was active during the reading tasks. MT was not used for ROI analyses but was defined to determine whether the temporal processing tasks activated MT and whether LOC and MT localizers activated the same regions.

3.3. Results

3.3.1. Behavioural data

Age-related normative performance was derived from previous results for the component reading tasks (Coltheart & Leahy, 1996; Edwards & Hogben, 1999; Partanen et al., submitted a) and temporal processing tasks (Partanen et al., submitted a). Z-scores based on normative performance were established for each participant. In order to eliminate extreme outliers, z-scores were set to a maximum value of ± 4. Outliers were shown on orthographic reading (1 dyslexic), dichotic pitch (2 dyslexics) and global motion (1 dyslexic, 1 average). Children with dyslexia demonstrated significantly lower scores than the average readers on the phonological and orthographic reading tasks, but not on dichotic pitch or global motion (see Table 3).   Additionally, scores on dichotic pitch and global motion were not significantly correlated, $r(13) = -.13$, $p > .50$.

Table 3. Mean (and *SD*) *z*-scores for reading and temporal processing measures

Measure	Average readers	Dyslexic readers	t (df = 11)
Phonological reading [a]	.35 (.45)	-1.81 (1.34)	3.16 *
Orthographic reading	.34 (.98)	-2.83 (1.23)	5.01 *
Dichotic pitch [a]	.06 (1.00)	.01 (3.27)	.04
Global motion	-.86 (1.52)	-1.69 (1.69)	.88

[a] Equal variances not assumed; *Groups significantly different, $p < .05$.

In order to determine whether temporal processing ability can predict component reading ability, regression analyses were conducted on the *z*-scores. The first set of analyses utilized phonological reading as the dependent variable and dichotic pitch and global motion were entered as separate predictors in the model. Results demonstrated that neither dichotic pitch [*F change* (1, 11) = 3.29, *p* > .05] or global motion [*F change* (1, 10) < 1] were significant predictors of phonological reading. Similarly for orthographic reading, dichotic pitch [*F change* (1, 11) < 1] and global motion [*F change* (1, 10) < 1] were not significant predictors.

3.3.2. Functional MRI data

3.3.2.1. In-scanner accuracy

Accuracy was recorded for the reading and temporal processing tasks while in the scanner. As previously described, tasks were designed with a parametric variation with easy, difficult and random conditions. A 2 group (average, dyslexic) x 3 condition (easy, difficult, random) between-within subjects ANOVA was conducted to establish differences between groups or conditions in accuracy scores. The four tasks were examined in separate ANOVAs, as the participants were instructed to respond differently across the tasks. Figure 9 illustrates the accuracies for the different tasks and conditions.

In phonological reading, there was no interaction between group and parametric condition, *F* (1.43, 15.68) = 1.59, *p* > .05 [degrees of freedom adjusted with Greenhouse-Geisser for non-spherical data, Mauchly's test, *p* < .15]. There was a significant effect of condition, *F* (1.43, 15.68) = 22.62, *p* < .001, but no differences between groups, *F* (1, 4.00) = 4.56, *p* > .05 [degrees of freedom adjusted with Brown and Forsythe's (1974) procedure for heterogeneous variances, Levene's test, *p* < .15]. Follow-up analyses for the effect of condition utilized a Bonferroni correction to adjust for multiple pairwise comparisons. Results showed that easy words were not significantly different from difficult words (*p* > .05), while both easy and difficult words had lower accuracies than false font symbols (both *p* < .05).

For orthographic reading, there was no significant interaction between group and parametric condition, *F* (2, 22) = 1.57, *p* > .05. There was a main effect of condition, *F* (2, 22) = 16.44, *p* < .001, but no differences between groups, *F* (1, 11) = 1.05, *p* > .05. Follow-

up pairwise comparisons with a Bonferroni correction demonstrated that easy words and false font symbols had higher accuracies than difficult words (both $p < .05$), but easy words and symbols were not different ($p > .05$).

For the dichotic pitch task, there was no interaction between group and condition, F (1.08, 11.87) < 1 [degrees of freedom adjusted with Greenhouse-Geisser for non-spherical data, Mauchly's test, $p < .15$]. There was a main effect of condition, F (1.08, 11.87) = 162.41, $p < .001$, but no difference between groups, F (1, 11) = 2.84, $p > .05$. Pairwise comparisons with a Bonferroni correction showed that SBR 10 (easy) and SBR 1 (difficult) were not significantly different in accuracy ($p > .05$), while both the easy and difficult conditions had higher accuracies than SBR 0 (random) (both $p < .05$).

Finally in the global motion task, there was no interaction between group and condition, F (1.15, 10.37) < 1 [degrees of freedom adjusted with Greenhouse-Geisser for non-spherical data, Mauchly's test, $p < .15$]. Similarly to the other tasks, there was a significant effect of parametric condition, F (1.15, 10.37) = 93.61, $p < .001$, but no differences between groups, F (1, 2.45) = 1.15, $p > .05$ [degrees of freedom adjusted with Brown and Forsythe's (1974) procedure for heterogeneous variances, Levene's test, $p < .15$]. Pairwise comparisons with a Bonferroni correction demonstrated that 85% coherence (easy) and 25% coherence (difficult) did not show differences in accuracy ($p > .05$), while both of these conditions had higher accuracies than 0% coherence (random) (both $p < .05$).

Figure 9. In-scanner accuracies for fMRI reading and temporal processing tasks
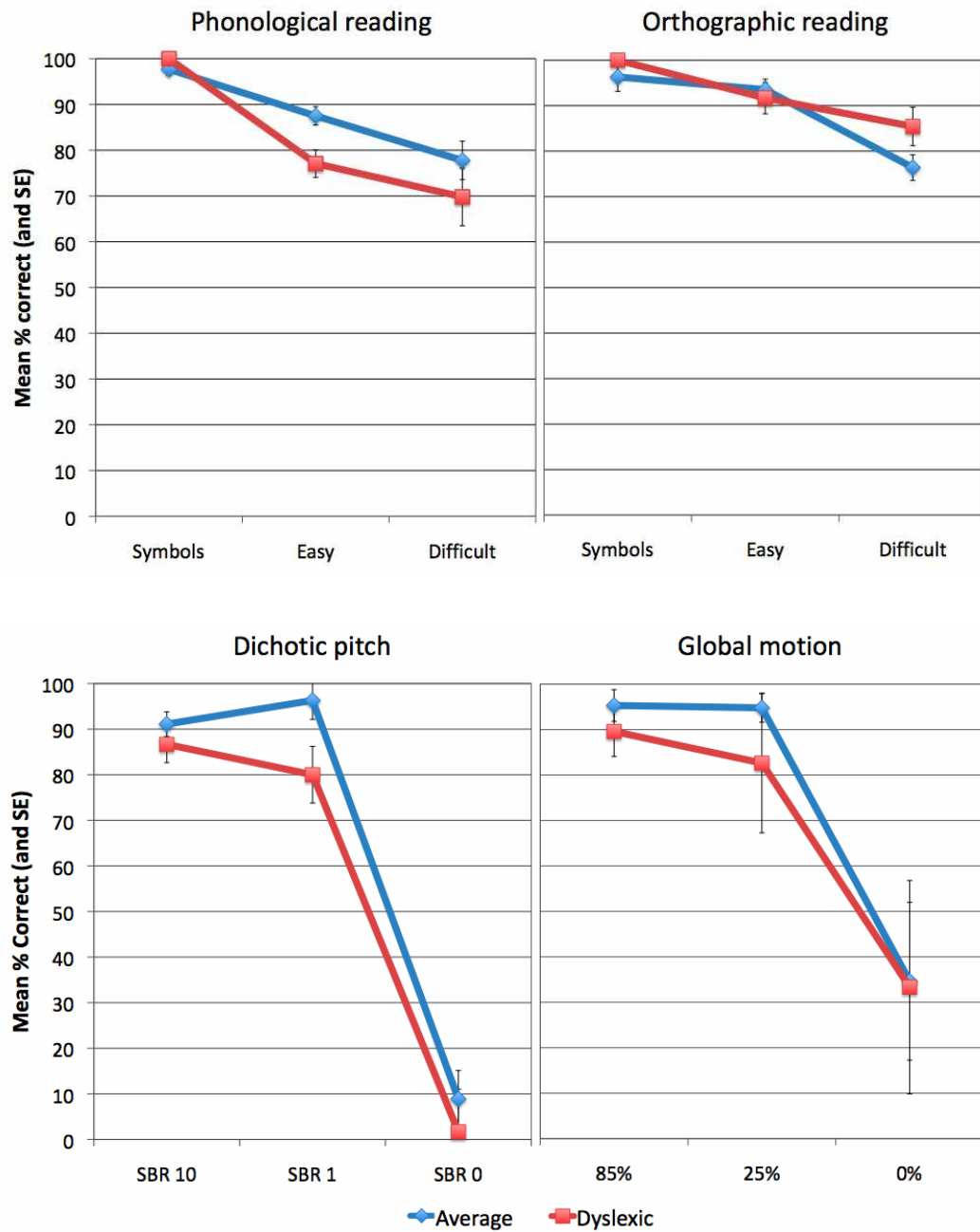
3.3.2.2. Whole-brain voxel-wise activity

Cortical activity for the MT localizer task was derived as the difference between moving and stationary dots. Increased activity for moving dots was observed bilaterally in the temporal-parietal-occipital cortex, as well as in putative visual areas V1 and V2. MT was defined for each participant in the temporal-parietal-occipital junction.

In the LOC localizer task, activity was defined as the difference in cortical activation obtained for unscrambled and scrambled pictures. Increased activity for the unscrambled pictures was observed bilaterally in the lateral occipital cortex, inferior temporal gyrus and fusiform gyrus. LOC was defined as the active region within lateral occipital cortex. Some participants demonstrated more than one cluster of activated voxels in this region; these were averaged together within a hemisphere for subsequent ROI analyses. Left and right LOC regions were established for each participant. Additionally, the MT and LOC tasks did not activate the same cortical areas; LOC for all participants was located posterior and inferior to MT. Figure 10 illustrates the activation maps for MT and LOC localizers for two participants. Activation maps for all participants are shown in Appendix G.

For dichotic pitch, cortical activity was initially established as the difference between all auditory conditions (SBR 10, 1, and 0) and the silent baseline. Significant increased activity for auditory conditions was observed in bilateral regions of Heschl's gyrus and superior temporal gyrus. Some participants demonstrated more than one cluster of activated voxels for this task and thus, these clusters were averaged within a hemisphere for ROI analyses. Bilateral dichotic pitch regions were established for each participant. Whole-brain contrasts between the auditory conditions (i.e., SBR 10 vs. SBR 0; SBR 1 vs. 0; SBR 10 vs. 1) did not illustrate significant differences in activity in individual participants.

In the global motion task, cortical activity was derived by the difference in activation obtained for moving dot conditions (85%, 25%, and 0%) and the stationary dot baseline. Increased activity for moving dots was displayed in bilateral regions of MT and putative V1 and V2. Further contrasts (85% vs. 25%, 85% vs. 0%, and 25% vs. 0%) illustrated increased activity in bilateral inferior and superior parietal lobules, left posterior middle temporal gyrus and left superior temporal sulcus. Similar to the other tasks, some participants demonstrated more than one cluster of activated voxels. These clusters were averaged together within a hemisphere for ROI analyses. Bilateral regions of global motion were established for each

participant. Figure 11 illustrates the activation maps for the dichotic pitch and global motion tasks for two participants. Activation maps for all participants are shown in Appendix G.

For the phonological and orthographic reading tasks, the contrast of interest was the difference between words (easy and difficult) and false font symbols. This contrast would demonstrate the cortical areas that were involved with reading but not necessarily with word form (i.e., form for symbols is the same as for words). In children with average reading ability, increased activity for phonological reading was shown in the left inferior, middle and superior frontal gyri, bilateral intraparietal sulci and lateral occipital regions. Children with dyslexia demonstrated similar activity to those of average readers, with the exception of increased activity in the right inferior and middle frontal gyri. The orthographic reading task showed similar activity to phonological reading; however direct comparisons between reading tasks or groups were not conducted as these were not of interest at this stage. ROI analyses determined activation differences between tasks and groups (discussed below). Figure 12 illustrates the activation maps for phonological and orthographic reading for two participants. Activation maps for all participants are shown in Appendix G. Appendix H lists ROI details for LOC, dichotic pitch and global motion for each participant.

Figure 10. Activation maps for MT and LOC localizer tasks
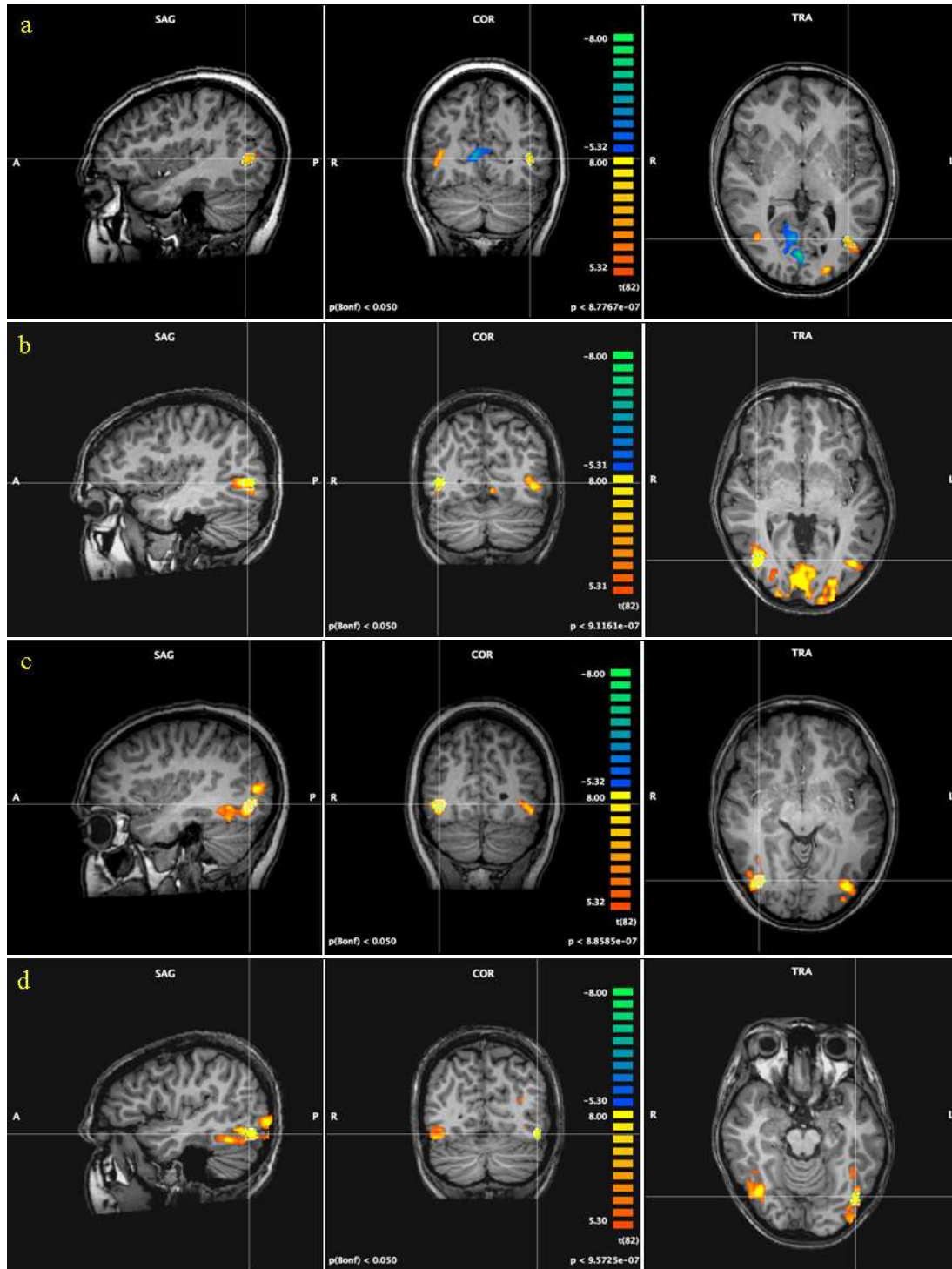
Activation for MT task (moving vs. stationary dots) is shown in average reader C04 (panel a) and dyslexic reader E02 (panel b); LOC activation (unscrambled vs. scrambled pictures) is shown in C04 (panel c) and E02 (panel d). Images are in radiological convention (left is right). Increased activity from baseline is depicted in yellow scale, decreased activity in blue ($p < .05$, corrected).

Figure 11. Activation maps for dichotic pitch and global motion tasks
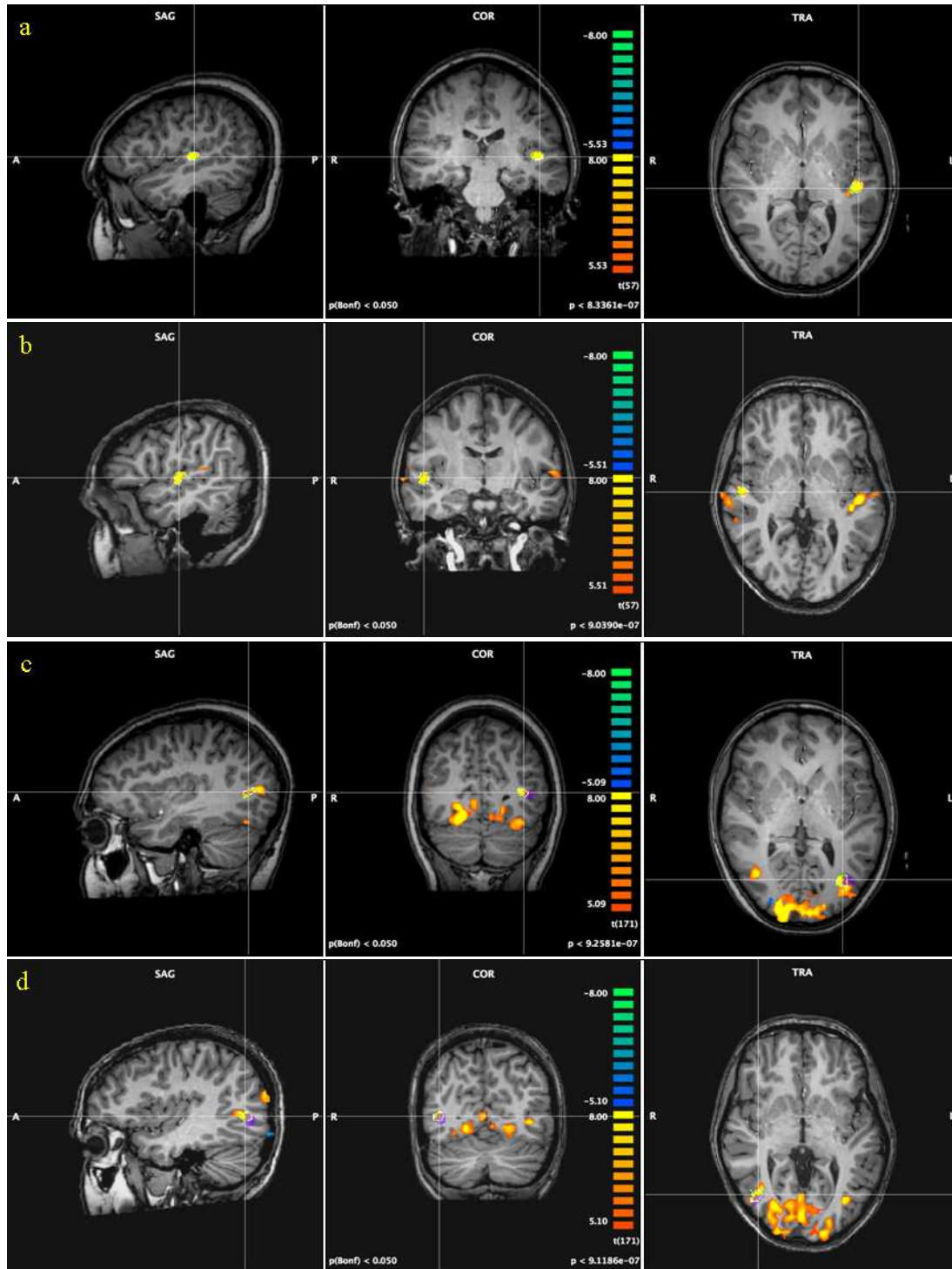
Activation for dichotic pitch (all auditory conditions vs. silent baseline) is shown in average reader C04 (panel a) and dyslexic reader E02 (panel b); global motion activation (all moving dots vs. stationary dots) is shown in C04 (panel c) and E02 (panel d) with area MT shown in purple. Images are in radiological convention (left is right). Increased activity from baseline is depicted in yellow scale, decreased activity in blue ($p < .05$, corrected).

Figure 12. Activation maps for phonological and orthographic reading tasks
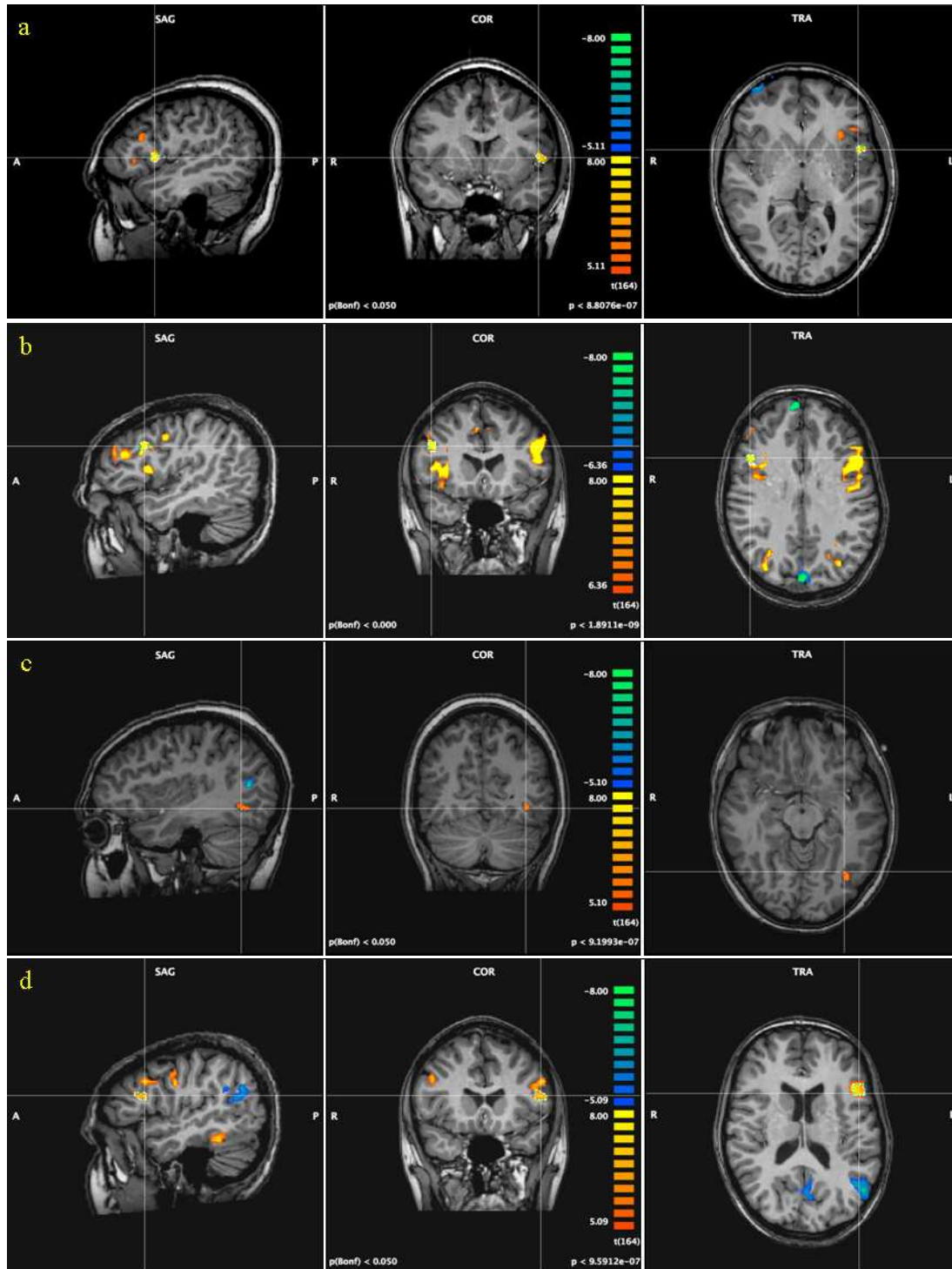
Activation for phonological reading (easy and difficult words vs. symbols) is shown in average reader C04 (panel a) and dyslexic reader E02 (panel b); orthographic reading activation (easy and difficult words vs. symbols) is shown in C04 (panel c) and E02 (panel d). Images are in radiological convention (left is right). Increased activity from baseline is depicted in yellow scale, decreased activity in blue (*p* < .05, corrected).

3.3.2.3.   ROI analyses

Cortical activity during the reading tasks was established within the six ROIs (bilateral LOC, dichotic pitch and global motion) for each participant. This was completed as follows: regression analyses were conducted using cortical activity from the phonological and orthographic reading tasks as separate dependent variables. Predictors of activity included easy words, difficult words and false font symbols. Within one ROI, a mean standardized β coefficient was established for each predictor; this was used as a function of cortical activity. Eighteen standardized β coefficients were identified per participant per reading task (3 ROIs in 2 hemispheres and 3 word condition predictors).

The β coefficients were analyzed using a 2 group (average, dyslexic) x 3 ROI (LOC, dichotic pitch, global motion) x 2 hemisphere (left, right) x 3 word condition (easy, difficult, symbols) between-within subjects ANOVA. Phonological and orthographic reading tasks were examined separately. In phonological reading, results demonstrated that there was an interaction between ROI, word condition and group, $F(4, 44) = 2.98$, $p < .05$. Simple-effect analyses compared the effect of group and the interaction between ROI and word condition; a Bonferroni correction was used to adjust for multiple comparisons. These results showed that there was no difference between groups in LOC at any of the word conditions (all $p > .05$), and there was no difference between word conditions in LOC ($p > .05$). In the dichotic pitch ROIs, there were no group differences at any of the word conditions ($p > .05$). Easy words demonstrated less activity than both difficult words and symbols in dichotic pitch regions ($p < .05$), while difficult words and symbols were not different from each other ($p > .05$). However, it was shown that in the global motion ROIs, children with dyslexia showed significantly greater activity than average readers but only on difficult words ($p < .05$). No differences between groups were shown on easy words or false font symbols in global motion regions ($p > .05$). Graphs depicting these data are shown in Figure 13.

An additional interaction shown in the phonological reading task was between ROI, hemisphere and group, $F(2, 22) = 5.73$, $p < .05$. Simple-effect analyses with a Bonferroni correction demonstrated that for average readers, left hemisphere regions in LOC had greater activity than right hemisphere regions ($p < .05$). However there were no differences between hemispheres in dichotic pitch or global motion ROIs ($p > .05$). In the dyslexic reader group,

there were no hemispheric differences in any of the ROIs of LOC, dichotic pitch or global motion (all $p > .05$).

The final analyses for phonological reading were to determine whether activity in the ROIs were significantly different than zero. The previous ANOVA analyses showed that there were differences between groups and word conditions but this does not indicate whether cortical activity was greater or less than baseline conditions. In these analyses, single-sample t-tests were conducted on the ROIs against a test value of zero. A Bonferroni-corrected α of .05 was used to correct for multiple comparisons. In LOC regions, results from the β coefficients (above) indicated that there were no differences between groups or word conditions and thus, these were averaged to formulate β coefficients for left and right LOC. Results demonstrated that both left LOC, $t(12) = 11.44$, $p < .05$, and right LOC were significantly greater than baseline conditions, $t(12) = 5.24$, $p < .05$. Secondly in the dichotic pitch ROIs, groups and hemispheres were analyzed together since they demonstrated no significant differences. Results showed that activity in the dichotic pitch ROIs were not different than baseline conditions in any of the word conditions (all $p > .05$). Finally, for the global motion ROIs, groups and word conditions were analyzed separately because there was a significant interaction between these factors. In the average reader group, none of the global motion regions (left and right) or word conditions (easy, difficult, symbols) were significantly different than baseline conditions (all $p > .05$). However in the dyslexic reader group, they demonstrated significantly greater activity than baseline in the right global motion ROI for difficult words, $t(3) = 6.45$, $p < .05$. All other regions or word conditions were not significantly different than baseline for dyslexic readers ($p > .05$).

Figure 13. Mean standardized β coefficients predicting cortical activity in phonological reading within ROIs
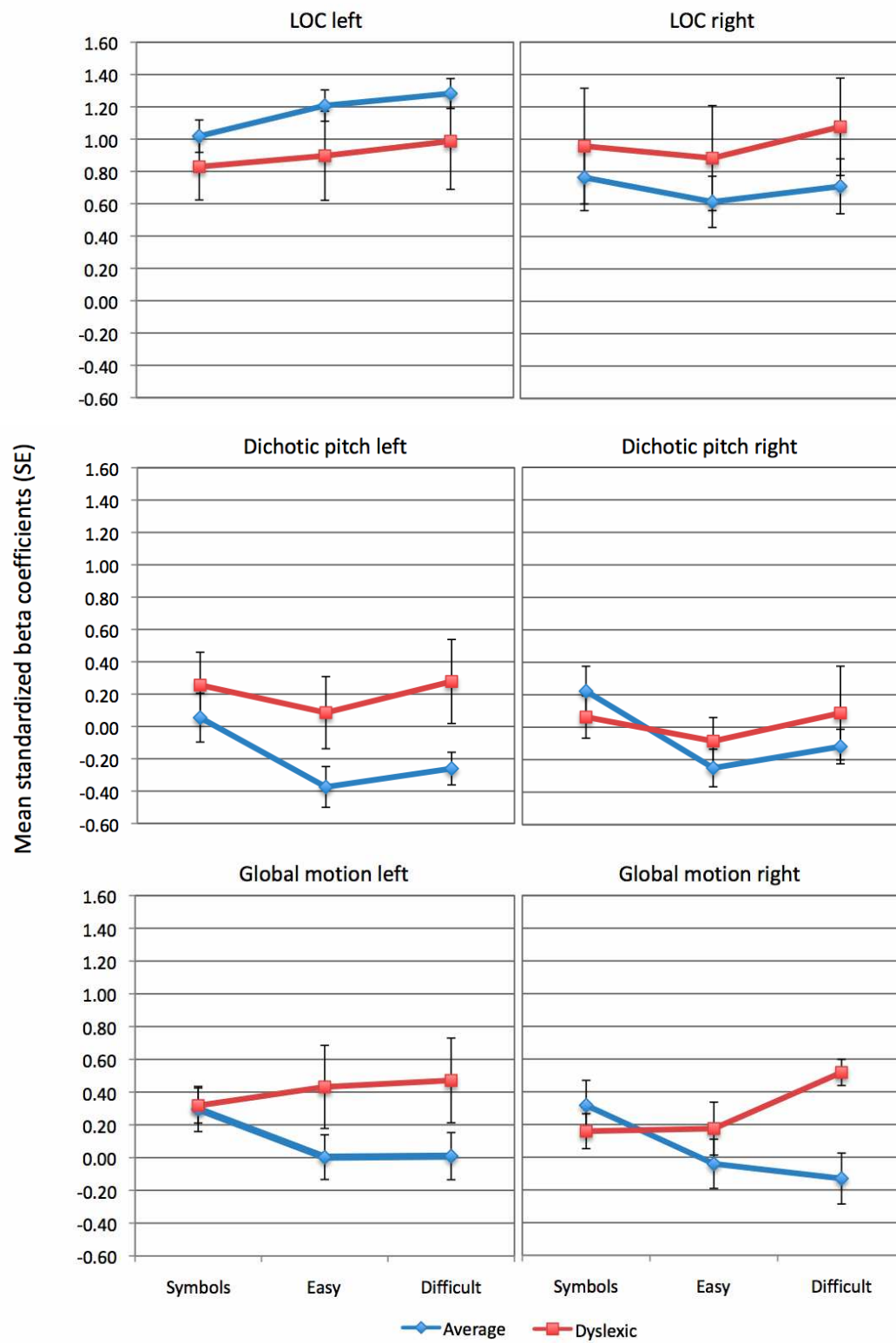
Analyses for the orthographic reading task were completed utilizing the same ANOVA design from the phonological reading task. These results showed there were no significant interactions between any of the conditions or groups. There was a main effect of ROI, $F(2, 22) = 54.18$, $p < .001$, but no effect of hemisphere, $F(1, 11) < 1$, $p > .50$, no effect of word condition, $F(1.19, 13.10) < 1$, $p > .50$ [degrees of freedom adjusted with Greenhouse-Geisser for non-spherical data, Mauchly's test, $p < .15$], or no effect of group, $F(1, 11) < 1$, $p > .50$. Follow-up pairwise comparisons with a Bonferroni correction determined that LOC had greater activity than both dichotic pitch and global motion ROI ($p < .05$), while there were no differences between the latter ($p > .05$). Graphs depicting these data are shown in Figure 14.

Single-sample t-tests with a Bonferroni correction were conducted to determine whether activity in the ROIs was different from baseline conditions. Analyses for all ROIs were conducted using averages of groups, hemispheres and word conditions as the previous ANOVA results demonstrated there were no differences between these variables. In LOC, activity was significantly greater than baseline conditions, $t(12) = 10.86$, $p < .05$. However the dichotic pitch and global motion ROIs were not significantly different than baseline ($p > .05$).

Figure 14. Mean standardized β coefficients predicting cortical activity in orthographic reading within ROIs
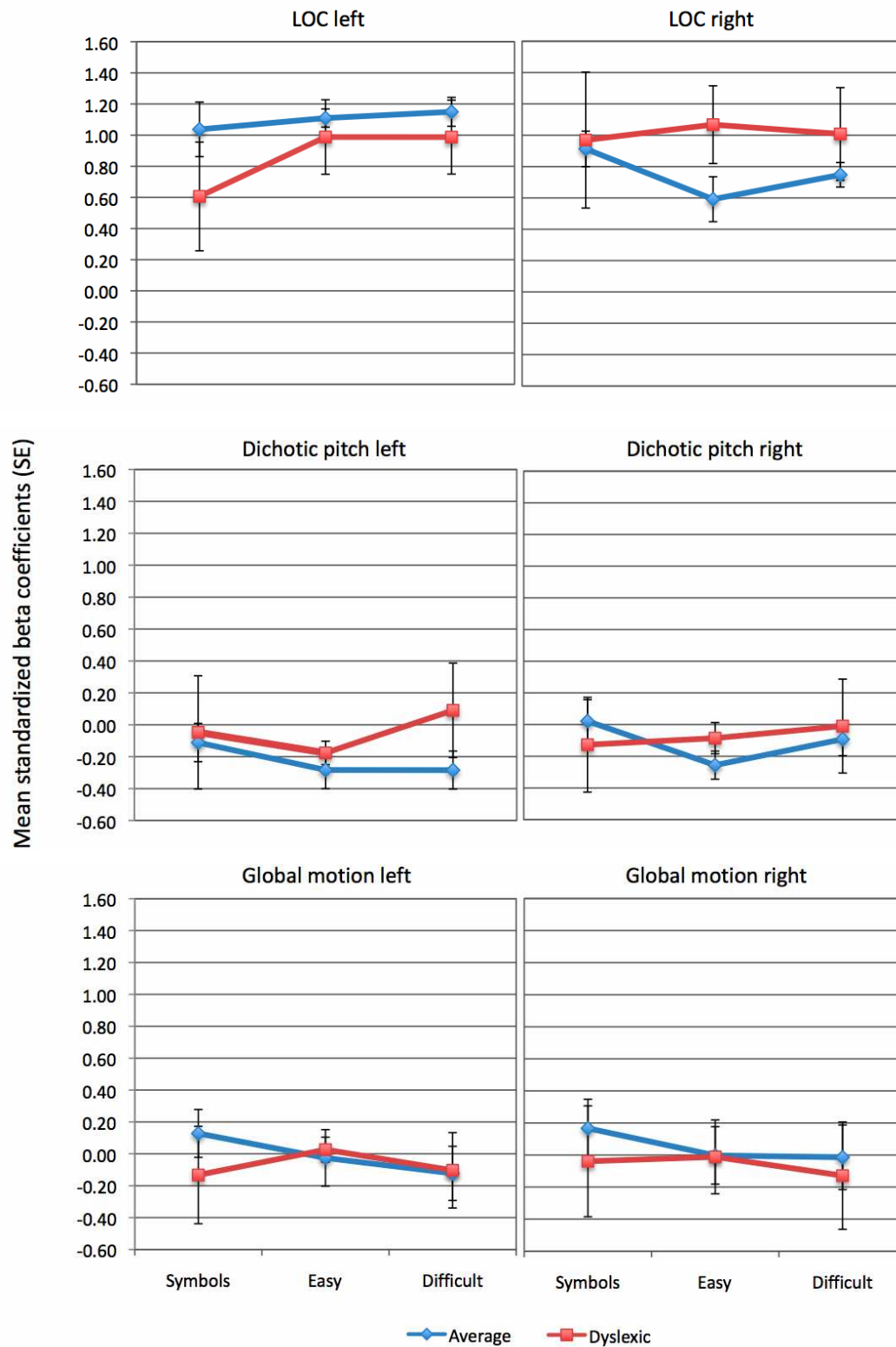
3.4. Discussion

3.4.1. Component reading and temporal processing abilities

Behavioural results showed that children with dyslexia obtained lower scores than average readers on measures of phonological and orthographic reading. This is in accordance to previous findings, which have suggested that dyslexic populations have deficits in both phonological and orthographic processing (Castles & Coltheart, 1993; Partanen et al., submitted a). Children with dyslexia may have difficulty in establishing a mental lexicon of words (orthographic processing) in addition to associating sounds to letters (phonological processing). The current results support the hypothesis that both of these component reading processes are affected in dyslexia.

In the temporal processing tasks, the dyslexic reader group was not different than the average reader group in tasks of dichotic pitch and global motion perception. Several studies have shown that only a proportion of persons with dyslexia have deficits in auditory or visual temporal processing (Edwards et al., 2004; Everatt, Bradshaw, & Hibbard, 1999). Inspection of thresholds in the current study, however, illustrates that most of the children with dyslexia presented poor global motion ability ($z < -1$). The lack of significant results is likely due to small sample sizes and thus, there was insufficient statistical power to elucidate differences between groups. The majority of children demonstrated average dichotic pitch thresholds ($z > -1$) and there was no correlation between dichotic pitch and global motion ability. Previous research has shown that children with dyslexia have deficits on auditory or visual temporal processing tasks, but not both (Edwards et al., 2004). In light of these results, it implies that the current sample of children tended to have poorer visual temporal processing ability than auditory temporal processing ability. Further research with larger sample sizes is needed to determine whether dyslexic readers can be classified into groups based on global motion or dichotic pitch perception deficits.

The current results also suggest that perceptual abilities in dichotic pitch and global motion do not predict phonological and orthographic reading ability. These results are supported by evidence that auditory temporal processing was not related to phonological reading (Heiervang & Hugdahl, 2003) and visual temporal processing was not related to orthographic reading (Amitay et al., 2002). The majority of studies, however, have determined some relationship between temporal processing and reading abilities (Booth et al.,

2000; Cestnick & Jerger, 2000; Talcott et al., 1999; Talcott et al., 2000b). Recent findings from our lab have illustrated that the relationship between component reading and temporal processing may vary depending on the age group (children or adults) and general reading ability (average or dyslexic) (Partanen et al., submitted a). Therefore, the current findings may be explained by an inability to adequately parse apart the average and dyslexic reading groups because of small samples. Further studies are needed to determine whether reading and temporal processing are related within the adolescent age group.

3.4.2. Parametric variation of difficulty

One goal of this thesis was to determine whether varying task difficulty would affect in-scanner accuracies or observed cortical activity in the ROIs. In phonological reading, it was shown that accuracy was similar between the easy and difficult word conditions. This suggests that similarity to the correctly spelled word (established from Experiment 1) may not have been the best factor for increasing task difficulty, at least in the context of the fMRI phonological reading paradigm. Other variables such as the number of phonemes or syllables in a word may be more predictive of phonological difficulty (Liberman & Shankweiler, 1985; Snowling, 1981).   However, there was also a greater variability in accuracy scores for the difficult words than the easy words suggesting that performance was less consistent for the more difficult condition. With a larger sample, this variability may decrease and modulation based on task difficulty may become more apparent in the phonological reading accuracy scores.

In the orthographic reading task, difficult words had lower accuracies than easy words and false font symbols. These results suggest that the parametric variation of grade-level was acceptable for the orthographic reading fMRI task. Previous studies have utilized word frequency to vary difficulty in orthographic reading tasks (Olson et al., 1984). The present study illustrates that grade-level for word acquisition may be another factor in predicting difficulty of orthographic reading in children.

In the dichotic pitch and global motion tasks, there were no differences in accuracy between the easy and difficult conditions, yet both had higher accuracies than the random conditions as expected. Previous results have shown accuracy differences between easy and difficult conditions for the same global motion task in adults (Giaschi et al., 2007). In the

current results, however, there was large variability in the difficult condition, which may explain the lack of significant results. Additionally, it is possible that the levels were not sufficiently difficult to elicit differences in accuracy. In the global motion task, stimuli were presented for a duration of 14 s at fixed difficulty levels and the participant may have obtained high accuracies because of this mode of stimulus presentation. For instance, in the psychophysical paradigms stimuli were presented using a staircase method which became more difficult with each successively correct answer. Absolute thresholds from the staircase method could be lower (i.e., < SBR 1 or < 25% coherence) than the levels chosen for the fMRI difficult conditions (SBR 1 for dichotic pitch and 25% motion coherence for global motion). Future studies may choose to utilize even lower coherence thresholds to elicit differences in accuracy between the easy and difficult conditions.

Since there were no differences between groups in accuracy scores for any of the tasks performed in the scanner, any differences observed in cortical activity cannot be explained by the tasks being more difficult for the dyslexic readers. The parametric fMRI results are discussed in subsequent sections.

3.4.3. Whole-brain activity for localizers, temporal processing and reading

Two regions within the occipital cortex were functionally localized. Moving dot stimuli activated bilateral temporal-parietal-occipital junctions, which were identified as MT. These results were hypothesized and confirm previous findings showing that MT is utilized for motion perception (Dumoulin et al., 2000; Giaschi et al., 2007; Huk et al., 2002; Sunaert et al., 1999; Tootell et al., 1995; Zeki et al., 1991). In the LOC localizer task, unscrambled pictures activated bilateral regions of lateral occipital cortex, inferior temporal gyri and fusiform gyri. These results are supported by evidence that LOC tasks activate two separate regions: the lateral occipital and posterior fusiform gyri (Grill-Spector et al., 1999). Additionally, MT and LOC did not engage the same regions; LOC was located adjacent to, but more posterior and inferior to MT in all participants. Retinotopic mapping has shown that these two regions are both anatomically and functionally distinct, with MT primarily involved with motion perception and LOC involved with object perception (Sayres & Grill-Spector, 2008). Some evidence suggests that MT and LOC may overlap partially and the overlapping region is utilized for both motion and object perception (Kourtzi, Bülthoff, Erb,

& Grodd, 2002; Liu, Slotnick, & Yantis, 2004); however the area of overlap was small and was not observed in all participants. The current results suggest that MT and LOC are relatively distinct regions of the cortex.

In the dichotic pitch task, increased activity was shown in bilateral regions of Heschl's gyrus and superior temporal gyrus. It was hypothesized that these regions would be activated based on previous neuroimaging studies utilizing dichotic pitch tasks (Giaschi et al., 2000; Puschmann et al., 2010). Heschl's gyrus is the initial cortical location for incoming auditory information, which then proceeds to surrounding areas in the superior temporal gyrus (reviewed in Hackney, 1987). Pitch perception may be additionally localized to Heschl's gyrus, particularly in the right hemisphere (Krumbholz, Patterson, Seither-Preisler, Lammertmann, & Lutkenhoner, 2003; Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; Zatorre, Evans, & Meyer, 1994). However other results have suggested that rapid temporal processing of auditory stimuli may be localized to the left auditory cortex (Zatorre & Belin, 2001). In a similar dichotic pitch task, it was shown that cortical activity for dichotic stimuli was comparable between left and right lateral Heschl's gyri (Puschmann et al., 2010). It can be argued that activation in these regions was due to the sounds from the MRI scanner and not from the auditory stimuli. For instance, the current sparse sampling design utilized a 5 s silent period, which may have been an insufficient time period for the BOLD response from the scanner sounds to decrease before the auditory stimuli were presented. However, previous sparse sampling designs have utilized similar timing patterns (i.e., 5 s silent periods), which also showed significant activity within the auditory cortex (Chiu et al., 2005; Van den Noort et al., 2008). Taking all of these studies into consideration, it is likely that dichotic pitch is processed in bilateral auditory cortex. In the current experiment, activation differences between conditions (i.e., SBR 10 vs. SBR 1) were not observable in single participants. This may be the result of utilizing a less robust design of sparse sampling, which elicited fewer images per participant than with constant sampling. Conversely, it is possible that there is no specific cortical location responsible for processing the illusory perception of dichotic pitch; for instance, the combining of binaural information occurs initially in the superior olive in the brain stem (Hackney, 1987). Specifically, the medial superior olive responds to interaural time differences (Yin & Chan, 1990), which may be the

subcortical site for processing dichotic pitch. Further studies with auditory evoked potentials are needed to elucidate these claims.

For global motion stimuli, all moving dot conditions activated bilateral regions of MT, which supports previous findings (Eden et al., 1996; Giaschi et al., 2007). Contrasts between coherence conditions demonstrated increased activity in bilateral inferior and superior parietal lobules, left posterior middle temporal gyrus, left superior temporal sulcus and left superior occipital gyrus. These regions were more active during coherent motion conditions (85% and 25%) than during random motion (0%). Others have demonstrated increased activity for coherent motion in similar cortical regions, such as the superior temporal sulcus and intraparietal sulcus (Braddick et al., 2000). The current results also suggest that motion regions other than MT are involved with global motion perception.

Phonological and orthographic reading tasks activated similar cortical regions and thus will be discussed concurrently. In children with average reading ability, increased activity for words was shown in left inferior, middle and superior frontal gyri, bilateral intraparietal sulci and bilateral lateral occipital cortex. These results are partially supported by previous results indicating increased activity within inferior frontal and lateral occipital regions (Eckert, 2004; Fiez & Petersen, 1998; Shaywitz et al., 2006). The present study, however, also demonstrated increased activity within the intraparietal sulcus. Activation differences between studies may be attributed to variations in the reading tasks that were utilized. Previous phonological reading tasks have included rhyming pairs of non-words (Booth et al., 2004; Cao et al., 2006; Pugh et al., 1996; Shaywitz et al., 2002), while orthographic reading tasks have included case judgement (Pugh et al., 1996) and matching words based on spelling (Booth et al., 2004). The tasks in the current study utilized pseudohomophone judgement for phonological reading and spelling judgement for orthographic reading. It is possible that the current tasks were more difficult than those used previously, which may have increased activity within intraparietal regions. One role of the intraparietal sulcus is for visual attention (reviewed in Grefkes & Fink, 2005), which suggests that the reading tasks used in this experiment likely also stimulated attentional processing mechanisms.

Children with dyslexia demonstrated increased activity within right inferior and middle frontal gyri, in addition to areas indicated above. Previous studies have postulated

that increased activity in right inferior frontal cortex involves a compensatory mechanism, which results from a disruption in left parietal-temporal and occipital-temporal regions (reviewed in Shaywitz et al., 2006). Additionally, it has been reported that dyslexic readers had a larger right than left inferior frontal gyrus in comparison to average readers (Robichon, Levrier, Farnarier, & Habib, 2000). These findings suggest that hemispheric differences may contribute to the neural deficits shown in those with reading problems. The current study, however, did not conduct between-group comparisons of whole-brain activity as the analyses were focused on single-subject ROI analyses. The disparity between hemispheres within the ROIs is discussed further below.

3.4.4. Cortical activation patterns between ROIs and reading

The main objective of this thesis was to determine whether activity from reading and temporal processing tasks share some of the same cortical regions. ROIs within LOC, auditory temporal processing areas (dichotic pitch) and visual temporal processing areas (global motion) were established. LOC was not active during the temporal processing tasks, but was included to ascertain whether this region was activated during reading. Component reading tasks of phonological and orthographic reading are discussed separately.

3.4.4.1. Lateral occipital cortex and phonological reading

In phonological reading, there were interactions between ROI, word condition and reading group, as well as between ROI, hemisphere and reading group. Within LOC, there were no differences between word conditions or groups, and activity was significantly greater than baseline conditions. These results imply that LOC was utilized for phonological reading in both reading groups. However, since LOC was active for false font symbols as well as for real words, this suggests that LOC is utilized for word form and not specifically reading. Lateral occipital regions are involved with object shape perception and respond more to intact objects than to scrambled patterns (Grill-Spector, 2003; Vinberg & Grill-Spector, 2008). An adjacent region in the left fusiform cortex has been suggested to be unique for word processing, termed the visual word form area (Cohen et al., 2000, 2002). Increased activity within this region was shown for words but not for consonant strings. A few participants in the current study illustrated increased activity in the left fusiform cortex

for words in comparison to false font symbols. However, this was not consistent across all participants. Further research is needed to determine if both LOC and the visual word form area are active during reading tasks.

With these findings, one would assume that LOC is utilized for form while other regions such as visual word form area are utilized for reading. However, the current results showed that average readers had greater activity in the left than right LOC during the phonological reading task. For children with dyslexia, activity in LOC was similar between left and right hemispheres. It has been suggested that the left occipital-temporal cortex is involved with word reading and this region may be disrupted in dyslexia (Pugh et al., 2000). If LOC functions as part of the reading process, greater activity within the left hemisphere would be expected. The current results imply that bilateral LOC is utilized for form, while left LOC may also be involved with early word analysis. Children with dyslexia showed equivalent activity between left and right LOC, which indicates they may have a deficit in left lateral occipital regions. These results provide preliminary evidence for the involvement of left LOC in phonological reading; however this would need to be confirmed with studies utilizing larger sample sizes.

Finally, there were no differences between word conditions, which illustrates that cortical activity in LOC did not modulate with task difficulty during phonological reading. Previous research has shown that LOC activation is not affected by difficulty in visual working memory tasks (Song & Jiang, 2006), however others have shown that LOC responds according to emotional salience and working memory load (Gläscher, Rose, & Büchel, 2007). Regions such as the visual word form area may be modulated by word frequency and difficulty during a reading task (Kronbichler et al., 2004). It is possible that the LOC may not be specific to reading difficulty, but rather is an early cortical location for word analysis. After the LOC, subsequent processing may be completed in the visual word form area or other cortical regions. An additional consideration is that the in-scanner accuracies for the phonological reading task did not show differences between conditions. Therefore it is possible that the phonological task did not elicit changes in behavioural performance and also in cortical activity. Further research with additional participants will be able to determine whether both the LOC and visual word form area are modulated by task difficulty during reading tasks.

3.4.4.2. Auditory temporal processing regions and phonological reading

In the auditory temporal processing (dichotic pitch) regions, there were no differences in cortical activation between groups or hemispheres. Easy words elicited less cortical activity than difficult words or false font symbols, which suggests that activity in the auditory cortex was modulated by task difficulty. Previous evidence has shown that auditory regions are deactivated during difficult pitch memory tasks (Rinne, Koistinen, Salonen, & Alho, 2009). In the current results, however, none of the conditions were significantly different than baseline. Therefore it cannot be concluded that these regions were affected by difficulty of the reading task. Additionally, these results imply that cortical regions for phonological reading are not shared with auditory temporal processing.

However, phonological reading and auditory temporal processing may be related through white matter connectivity. Phonological reading activated inferior, middle and superior frontal gyri, while dichotic pitch activated Heschl's and superior temporal gyri. Through white matter tracts, Heschl's gyrus is connected with anterior and posterior regions of the superior temporal gyrus (Upadhyay et al., 2008), which is then connected to inferior frontal gyri via the arcuate fasciculus (Glasser & Rilling, 2008). Additionally, superior temporal gyrus connections to the inferior frontal gyrus were strongly left lateralized and overlapped with phonological activity (Glasser & Rilling, 2008). With these considerations in mind, the behavioural link shown between phonological reading and auditory temporal processing (Boets et al., 2006; Stein & McAnally, 1995; Talcott et al., 1999; Tallal, 1980; Witton et al., 2002) may be shown within white matter connections between superior temporal and inferior frontal gyri. Further research utilizing diffusion tensor imaging would elucidate whether white matter connectivity and integrity are important for phonological reading and auditory temporal processing.

3.4.4.3. Visual temporal processing regions and phonological reading

In the global motion ROI, an important characteristic emerged. The dyslexic reader group showed greater activity than the average readers, however, only for reading difficult words. There were no group differences for easy words or false font symbols. Furthermore, cortical activity in the right hemisphere for difficult words in dyslexic readers was significantly greater than baseline conditions. All other conditions for both reading groups

demonstrated similar activity to baseline. These results suggest that in average readers, the areas activated by global motion are not activated by phonological reading. On the other hand, children with dyslexia have similar regions activated between phonological reading and global motion during difficult reading conditions.

As discussed in previous sections, these activation differences between groups cannot be explained by differences in accuracy. One hypothesis is that persons with dyslexia require greater effort in both phonological reading and global motion perception tasks, which increases recruitment of attentional mechanisms and thus brain activity. During coherent motion conditions, increased activity was observed bilaterally in the inferior and superior parietal lobes, which are regions that may be activated during tasks requiring visual attention (reviewed in Culham & Kanwisher, 2001). Given these results, it is possible that dyslexic readers show common areas of activation for reading and temporal processing due to increased attentional demands for both of these tasks. This relationship was only shown within right hemisphere regions and some evidence suggests that the right parietal lobe is involved with directing attention to the left hemifield (Kastner & Ungerleider, 2000). The current paradigm presented stimuli at fixation and in both hemifields, therefore an increase in right parietal regions cannot be attributed to increased attention in the left hemifield. Other results have shown that persons with dyslexia may have a deficit in left temporal-parietal regions (Shaywitz et al., 2006) and thus the lack of similar activity between reading and temporal processing in the left hemisphere may be due to some disruption within these regions. It is therefore suggested that increased attentional processing may explain the similar activation patterns in right hemisphere regions used for phonological reading and visual temporal processing. Another hypothesis is that during difficult tasks, there is increased recruitment from brain regions that are not active during easy tasks. For instance, recruitment from the dorsolateral prefrontal cortex has been shown during difficult reasoning tasks (Kroger et al., 2002) and the frontal and posterior parietal cortices during difficult working memory tasks (Paskavitz et al., 2009). It is suggested that in dyslexic readers, the increased activity shown in right MT and parietal regions may be due to recruitment from these areas due to task difficulty. This is the first evidence that visual temporal processing and phonological reading could involve similar cortical regions, at least in a reading impaired

population. This pattern, however, may be due to the recruitment of similar cortical areas driven by visual attention mechanisms common to both tasks.

Finally, these results also provide evidence for brain regions that are modulated by task difficulty. Increased cortical activity was only observed during a difficult reading condition for children with dyslexia, which suggests that right MT and parietal regions may be engaged only during difficult tasks. Previous results have shown that bilateral parietal and occipital-temporal regions illustrate increased activity when words become more degraded and thus more difficult to perceive (Cohen, Dehaene, Vinckier, Jobert, & Montavont, 2008). The current results suggest that a pseudohomophone judgement task also elicits changes in brain activity according to difficulty. Additional participants are needed to provide more definitive evidence that visual temporal processing regions are modulated by task difficulty during phonological reading.

3.4.4.4. ROIs and orthographic reading

During the orthographic reading task, there was increased activity within bilateral LOC. In contrast to the phonological reading task, there were no differences between left and right LOC for either reading group. These results suggest that LOC may be involved with word form during orthographic reading and early word analysis during phonological reading. This provides additional evidence that phonological and orthographic reading may be processed in separate regions of the cortex (Jobard et al., 2003). Additionally, the phonological reading task may be more difficult than the orthographic reading task and this may lead to increased activity within early visual areas due to top-down attentional processing (Kastner & Ungerleider, 2000). However since LOC is active for both reading tasks, the current results suggest that this region is one component of reading, such as in analyzing word form or structure.

In the auditory temporal processing regions, cortical activity was not different from baseline conditions. These results indicate that there are likely no similar cortical regions involved in auditory temporal processing and orthographic reading. However, a relationship in white matter connectivity between regions utilized for dichotic pitch and orthographic reading cannot be ruled out, as discussed previously in relation to phonological reading.

Also in the global motion regions, cortical activity during the orthographic task was alike to the baseline condition. These findings suggest that the regions activated by global motion are not involved in orthographic reading. Since there were common activation patterns between global motion and phonological reading in children with dyslexia, the lack of a relationship with orthographic reading supports the idea that component reading may involve separate cortical pathways (Jobard et al., 2003). However in the current sample, children with dyslexia are enrolled in remediation programs that are primarily focused on phonology. Similar regions between temporal processing and phonological reading, but not orthographic reading, may be explained by a compensatory mechanism that increases through phonological training. Although this was not explicitly examined, future research may associate the type of training program to cortical activity shown in phonological and orthographic reading tasks.

Finally, there were no significant effects of word condition in any of the ROIs. These results imply that for orthographic reading, none of the specified cortical regions were modulated by task difficulty. This is in contrast to the in-scanner accuracies for the orthographic task, which demonstrated higher accuracies for the easy words and symbols than for difficult words. However it is possible that brain areas that were not included in this experiment are influenced by task difficulty (i.e., visual word form area, Kronbichler et al., 2004). Future research with additional participants may determine that other cortical regions are moderated by difficulty in the orthographic reading task.

3.4.4.5. Considerations of ROI analyses

An alternative method of determining whether reading and temporal processing tasks activated similar regions would be by means of a conjunction analysis. However, conjunction analyses may have been positively biased towards tasks that included more trials (i.e., global motion) or longer trials (i.e., phonological and orthographic reading). The current method of establishing ROIs within single participants was chosen to be more conservative, as there would be no bias in cortical activity towards a particular task.

4. CONCLUSIONS

The main objective of this thesis was to determine if the regions activated by temporal processing are also activated by reading in children with average reading ability and in children with dyslexia. It was hypothesized that average readers would have some of the same regions activated for reading and temporal processing, while dyslexic readers would have abnormal activity within these regions. The current results do not support these hypotheses. There was no evidence for commonly activated regions between auditory temporal processing and reading in either the average or dyslexic reader group. However, there were similar activation patterns between right visual temporal processing areas and phonological reading. This was only demonstrated for children with dyslexia during difficult reading conditions. It was suggested that dyslexic readers have increased attentional resources deployed during visual temporal processing and phonological reading, as well as increased recruitment from these regions during difficult tasks, and this may explain the cortical relationship shown between temporal processing and reading. Additionally the dyslexic readers may have a disruption in left hemisphere areas utilized for visual temporal processing. The current findings showed that children with average reading ability likely do not have similar regions engaged during reading and temporal processing, while children with dyslexia may have similarly activated regions between phonological reading and visual temporal processing. Further research is needed with larger sample sizes to determine whether this is a consistent effect for both groups.

The second objective of this thesis was to examine whether there were similar activation patterns between component reading and auditory or visual temporal processing. It was hypothesized that auditory temporal processing would share some of the same cortical regions as phonological reading, while visual temporal processing would activate similar regions as orthographic reading. The fMRI findings do not provide support for these hypotheses. In children with dyslexia, there were shared activation patterns between visual temporal processing and phonological reading. However, there were no similar regions activated between visual temporal processing and orthographic reading, which indirectly suggests that phonological and orthographic reading may be utilizing separate cortical systems. The current results suggest that there is not a modality-specific relationship between reading and temporal processing. Conversely, it is suggested that the shared regions

of activation may be due to increased attentional processing during difficult tasks. Additional participants are needed to elucidate these claims.

     The final objective of this thesis was to determine whether the lateral occipital cortex (LOC) was activated during the reading tasks. It was hypothesized that LOC would show increased activity during reading, as this region is typically utilized for object or shape perception. The current results provide preliminary support for these hypotheses. It was shown that LOC was active during phonological and orthographic reading, with increased activity in the left hemisphere for average readers during the phonological reading task. Children with dyslexia showed equivalent cortical activity between left and right regions for both reading tasks. This was proposed as evidence that LOC is involved in the reading process and that children with dyslexia may have a disruption in left lateral occipital regions.

     This thesis determined that some aspects of temporal processing and reading are utilizing the same cortical regions, however, only in children with dyslexia. These results provide novel preliminary evidence that a cortical relationship between reading and temporal processing may exist and also provides support for the involvement of temporal processing in the neural deficits underlying dyslexia.

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APPENDICES

Appendix A: Phonological reading lists for Experiment 1

One-word choice condition, Practice words

sloe	wrest	sope	heet
lesp	fote	noke	
nek	garb	thane	

One-word choice condition, Version A

bote	graip	shart	dait
ferst	broave	dight	terch
crail	kike	naim	warld
beaf	joak	rerding	howse
fairce	ponsil	thurd	stoan
femse	koff	gaim	parper
fethur	truk	bloe	ploice
reash	staib	derty	strate
flote	screem	beal	sait
deel	jenns	broun	hawl
nerr	hoam	roke	caim
chone	kliss	trine	thit
mennie	munnia	drawp	chare
cloun	kard	seef	wike
tupe	borb	bern	caive
sizocs	rofe	meeve	shaip
sede	grean	surch	mowse
dair	chikun	flere	fike
appul	crif	nale	braim
fane	gurp	kreen	hurp

Appendix A (continued)

One-word choice condition, Version B

kake	dorty	drawf	storn
fearce	daib	chakun	hoap
gralp	jeens	berk	stait
braik	scraum	sebe	plaice
cloon	belf	werld	sarch
kiff	derl	paim	reech
bord	teech	flore	leeve
chane	thord	caide	saif
fense	fithur	munnie	gome
blee	roap	broan	nennie
harl	strale	crie	thot
nall	seet	fite	farst
sizors	trub	roze	tipe
craul	reeding	chire	hoise
nowse	apput	wite	gurl
klass	paiper	holn	neer
kird	pensil	bofe	fone
bair	joaf	trane	shaup
braive	kight	kreem	daif
flole	shurt	greln	nain

Two-word choice condition, Practice words

peech / peef	wead / gead	mong / rong
graid / gralp	berf / berd	boik / baik
kam / kar	dorter / docter	
neet / nert	fead / feam	

Appendix A (continued)

Two-word choice condition, Version A

beal / bair	sede / sebe	staib / stait
flote / flole	roke / roze	bern / berk
joak / joaf	seef / seet	fike / fite
kike / kake	beaf / belf	dair / daif
fethur / fithur	surch / sarch	hurp / hoap
shart / shurt	naim / nain	caim / paim
mennie / nennie	crif / crie	trine / trane
hoam / holn	borb / bord	sizocs / sizors
fairce / fearce	appul / apput	chare / chire
ferst / farst	howse / hoise	flere / flore
screem / scraum	braim / braik	broave / braive
kreen / kreem	warld / werld	caive / caide
ponsil / pensil	bote / bofe	
crail / craul	grean / greln	

Two-word choice condition, Version B

gaim / gome	fane / fone	truk / trub
gurp / gurl	mowse / nowse	rerding / reeding
shaip / shaup	tupe / tipe	parper / paiper
chone / chane	terch / teech	graip / gralp
nerr / neer	drawp / drawf	thurd / thord
chikun / chakun	munnia / munnie	dait / daib
nale / nall	femse / fense	ploice / plaice
koff / kiff	stoan / storn	wike / wite
derty / dorty	sait / saif	strate / strale
reash / reech	bloe / blee	hawl / harl
kard / kird	deel / derl	thit / thot
dight / kight	kliss / klass	broun / broan
jenns / jeens	rofe / roap	
meeve / leeve	cloun / cloon	

Appendix B: Orthographic reading lists for Experiment 1

One-word choice condition, Practice words

toad	great	gane	stripe
faik	strange	woman	
shaid	beem	blok	

One-word choice condition, Version A

wize	anser	sensitive	alternitive
fought	engine	study	salad
wait	mysterey	need	reath
skait	basement	easy	dreem
demon	culpret	hevvy	taip
deap	evry	interesting	sleap
gote	backwords	rain	perched
resource	mussle	wheet	wurd
roar	face	lake	applause
store	assure	sammon	harth
travel	libberty	coat	pavement
grone	compliment	sheep	pleese
taik	scare	streat	reason
believe	choose	between	nice
dignity	hoal	wagon	explane
condence	trail	nostrels	trousers
fue	thum	importent	streem
keep	senaters	captain	nusance
sudden	hert	several	smoke
lurn	exsample	ghost	distence

Appendix B (continued)

One-word choice condition, Version B

goat	tape	goast	sleep
trale	wreath	purched	nuisance
suddin	few	hole	sheap
learn	smoak	captin	beleave
skate	eazy	wagun	liberty
deimon	every	resourse	condense
important	sevral	hurt	laik
sallad	culprit	travul	explain
backwards	chooze	baisment	fase
salmon	pavement	nise	intresting
keap	example	dignity	dream
aplause	wise	rane	deep
nead	hearth	please	stoar
grown	reeson	cote	answer
scair	nostrils	word	heavy
trowsers	rore	studdy	alternative
wheat	ashure	senators	thumb
faught	mystery	sensative	complimant
take	stream	wate	muscle
distance	enjine	betwean	street

Two-word choice condition, Practice words

rume / room	tertle / turtle	group / groop
boal / bowl	circus / sircus	threat / thret
young / yung	snoe / snow	
clown / cloun	wroat / wrote	

Appendix B (continued)

Two-word choice condition, Version A

sheep / sheap	senaters / senators	wheet / wheat
condence / condense	harth / hearth	resource / resourse
skait / skate	lake / laik	keep / keap
engine / enjine	choose / chooze	sammon / salmon
believe / beleave	hert / hurt	salad / sallad
reason / reeson	applause / aplause	hevvy / heavy
fue / few	demon / deimon	wurd / word
mysterey / mystery	hoal / hole	smoke / smoak
need / nead	streem / stream	culpret / culprit
distence / distance	several / sevral	explane / explain
sensitive / sensative	importent / important	interesting / intresting
scare / scair	roar / rore	wait / wate
wize / wise	sudden / suddin	
thum / thumb	reath / wreath	

Two-word choice condition, Version B

captain / captin	fought / faught	trail / trale
dreem / dream	rain / rane	between / betwean
store / stoar	assure / ashure	libberty / liberty
anser / answer	backwords / backwards	travel / travul
nostrels / nostrils	gote / goat	evry / every
taik / take	perched / purched	streat / street
face / fase	alternitive / alternative	pavement / pavemant
compliment / complimant	coat / cote	study / studdy
wagon / wagun	nice / nise	mussle / muscle
exsample / example	nusance / nuisance	taip / tape
deap / deep	grone / grown	pleese / please
easy / easy	trousers / trowsers	ghost / goast
sleap / sleep	dignaty / dignity	
basement / baisment	lurn / learn	

Appendix C: Mean (and *SD*) accuracy for Experiment 1 (% correct)

Word Condition	Orthographic reading		Phonological reading	
	Average readers	*Dyslexic readers*	*Average readers*	*Dyslexic readers*
One-word	89.02 (19.05)	75.16 (23.54)	88.50 (15.72)	75.94 (20.76)
Two-word	93.66 (15.96)	83.36 (20.91)	92.68 (11.36)	81.62 (20.88)

Appendix D: Standardized *β* coefficients for predicting reaction time and accuracy in phonological and orthographic reading tasks

Reading task (Reader group)	Dependent variable	Predictors	β	t
Phonological (Average)	Reaction time (sec)	Length	.10	.91
		Frequency	-.20	-1.38
		Grade level	-.21	-1.40
		Similarity [a]	.05	.44
	Accuracy (% correct)	Length	.13	1.17
		Frequency	.20	1.34
		Grade level	.31	2.15 *
		Similarity [a]	-.21	-1.93 *
Phonological (Dyslexic)	Reaction time (sec)	Length	-.00	-.01
		Frequency	-.04	-.29
		Grade level	-.26	-1.84
		Similarity [a]	.35	3.35 *
	Accuracy (% correct)	Length	.00	-.03
		Frequency	-.01	-.07
		Grade level	.10	.65
		Similarity [a]	-.24	-2.16 *
Orthographic (Average)	Reaction time (sec)	Length	.23	2.50 *
		Frequency	-.02	-.17
		Grade level	.25	2.37 *
	Accuracy (% correct)	Length	-.27	-2.93 *
		Frequency	-.02	-.25
		Grade level	-.24	-2.28 *
Orthographic (Dyslexic)	Reaction time (sec)	Length	.40	4.80 *
		Frequency	.08	1.00
		Grade level	.29	2.96 *
	Accuracy (% correct)	Length	-.17	-1.82
		Frequency	-.01	-.13
		Grade level	-.29	-2.74 *

* $p < .05$.
[a] Larger values on the similarity scale indicates that the phonological word was more
dissimilar than the correctly-spelled word.

Appendix E: Phonological reading lists for Experiment 2

Simulator list, Easy words for dyslexic readers

broun	stuk	bord	reech
yupe	loip	jumer	laype
seet	bistim	roik	deside

Simulator list, Easy words for average readers & Difficult words for dyslexic readers

creest	seber	spoak	tickel
awaik	graip	dair	bote
kird	harl	marpe	shern

Simulator list, Difficult words for average readers

thord	ponsil	phurn	cawler
strate	koff	dubble	thawt
weech	crif	nennie	loyste

Real list, Easy words for dyslexic readers

snoe	shoner	leeve	kake
nire	froane	tertle	grean
screem	waibe	truble	cleeme
prowd	trak	shob	joil
paike	lern	fipe	frend
fead	doarn	pleam	bofe

Real list, Easy words for average readers & Difficult words for dyslexic readers

shaip	hoap	cloon	flote
gend	nerr	daif	blaid
diline	surch	coide	terch
choap	sheabe	bottel	appul
middel	baish	paraid	maik
chaile	caim	kleeps	remane

Appendix E (continued)

Real list, Difficult words for average readers

erley	braime	pawkel	mennie
roaden	fithur	reash	phorme
brawt	bocks	pher	fairce
theape	chone	kwean	bekaws
paim	farst	dawler	kair
oashen	koad	heib	coim

Appendix F: Orthographic reading lists for Experiment 2

Simulator list, Easy words for dyslexic readers

hevvy	persen	table	name
number	nice	cold	ahedd
small	cote	blak	groe

Simulator list, Easy words for average readers & Difficult words for dyslexic readers

deimon	rore	hert	breth
beam	bownd	ghost	paist
drown	hole	meant	stripe

Simulator list, Difficult words for average readers

roab	frale	hoarse	grieve
advise	vaise	sneaze	hertle
boar	shreek	spoil	fiery

Real list, Easy words for dyslexic readers

flower	please	every	wait
fase	noyse	study	deep
rain	easy	grass	stait
laik	grait	answer	suddin
keap	meen	paiper	street
word	darke	sleep	erth

Real list, Easy words for average readers & Difficult words for dyslexic readers

reason	trale	skate	hoarn
sweap	giant	action	shor
dert	enjine	goat	wagun
statue	wheat	soop	chooze
staige	braik	jurney	scare
stream	wise	thumb	coal

Appendix F (continued)

Real list, Difficult words for average readers

rein	haist	brim	raid
spair	purch	crate	mortle
caip	gallery	chisle	yern
fome	civil	fabel	assure
cavern	carben	invaid	wreath
dread	fought	bushel	clerk

Appendix G: Activation maps for individual participants for all fMRI tasks

This appendix illustrates the whole-brain activation maps for each participant (C = control average reader; E = experimental dyslexic reader).

Images are shown in the axial (*z*) plane (18 images per participant per task) and in radiological convention (left is right). Talairach coordinates for each image are: (*x, y* = 0, 0) and (*z* = -34, -28, -22, -16, -10, -4, 2, 8, 14, 20, 26, 32, 38, 44, 50, 56, 62, 68).

Contrasts for each task are shown as follows:
> MT localizer: moving vs. stationary dots
> LOC localizer: unscrambled vs. scrambled pictures
> Dichotic pitch: all auditory conditions (SBR 10, 1, 0) vs. silent
> Global motion: all moving dots (85%, 25%, 0% coherence) vs. stationary dots
> Phonological reading: words (easy and difficult) vs. false font symbols
> Orthographic reading: words (easy and difficult) vs. false font symbols

Increased activity from baseline is depicted in yellow/orange scale, decreased activity in blue/green scale.

P-values are shown as uncorrected (p) and with a Bonferroni correction (p Bonf).

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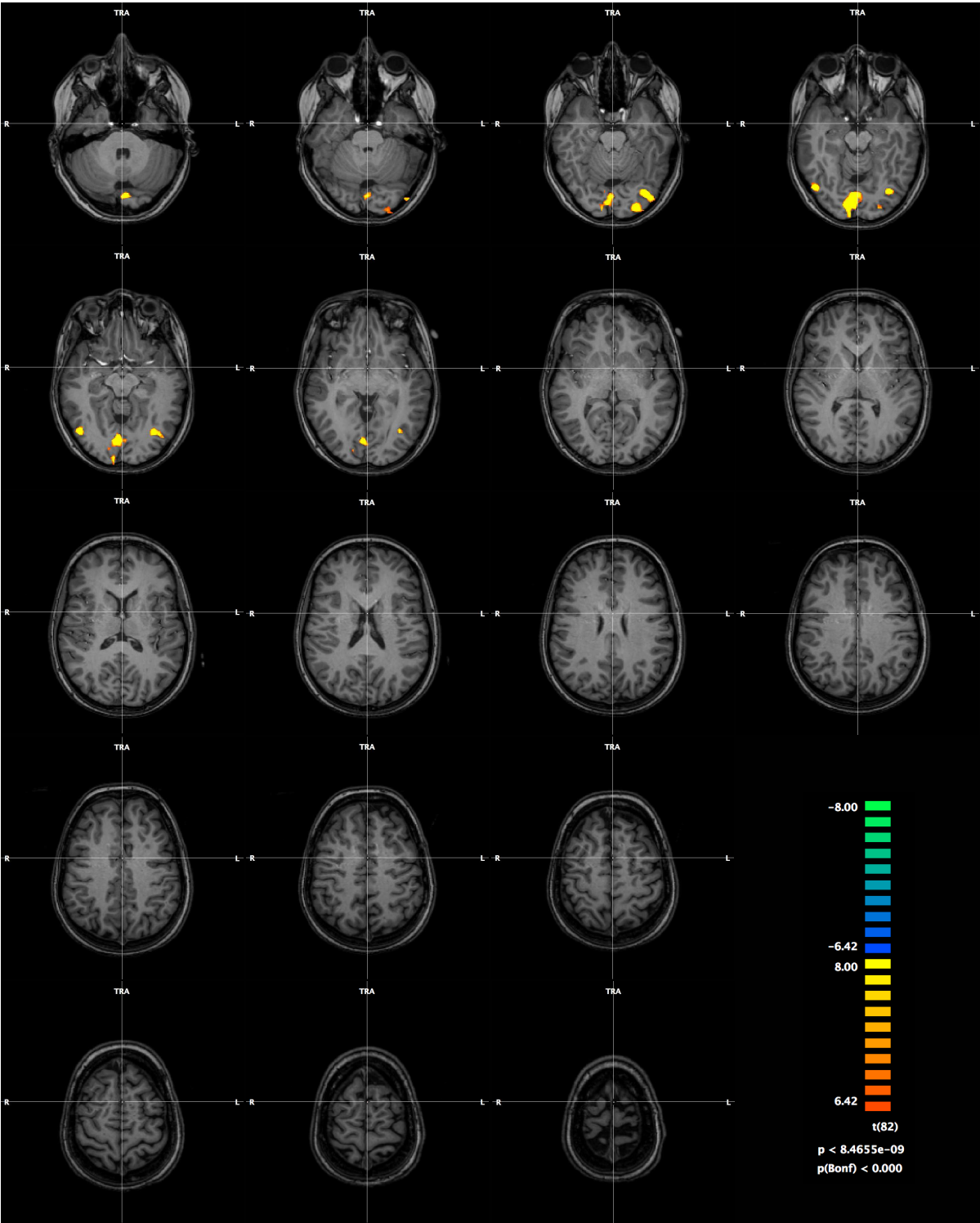
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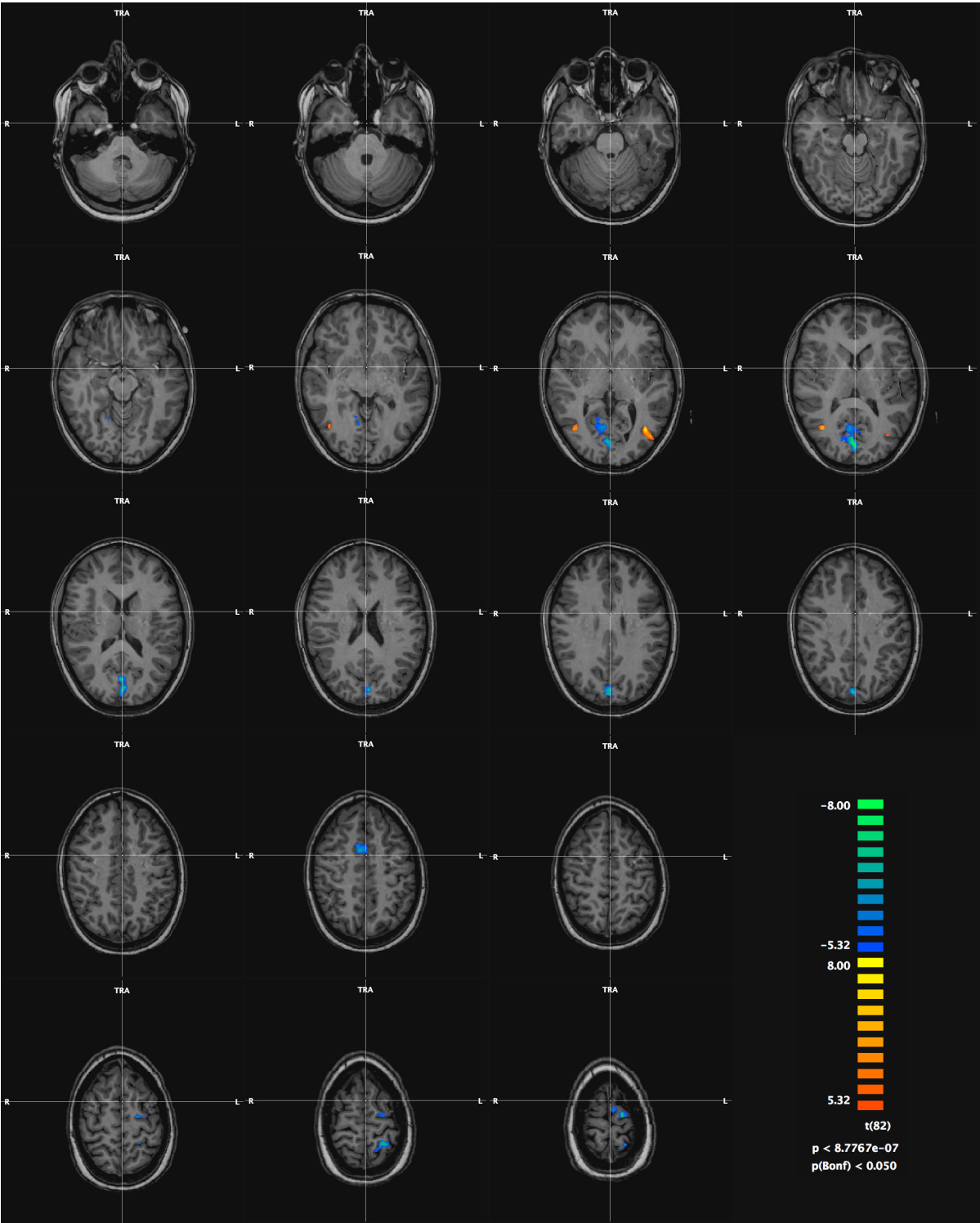
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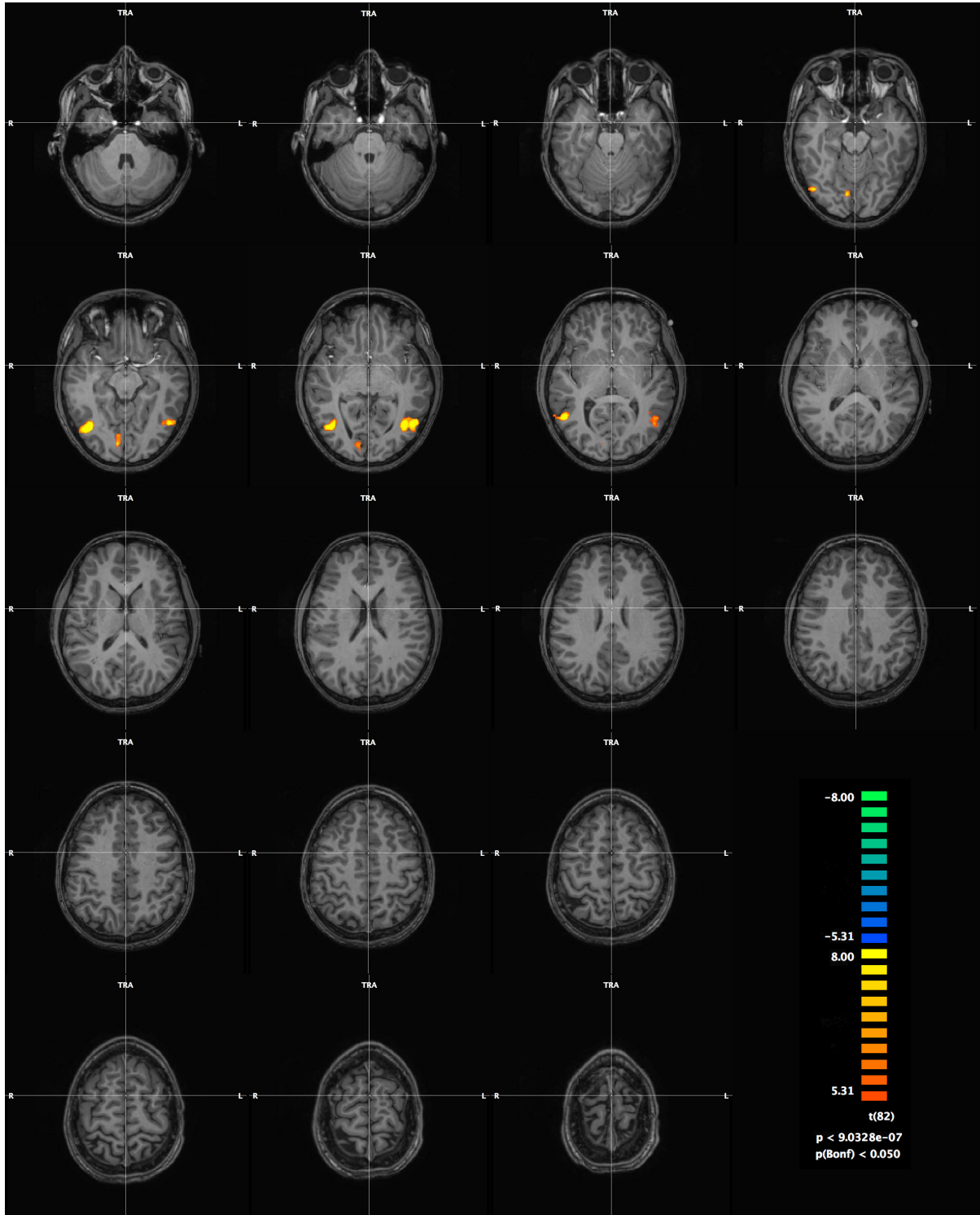
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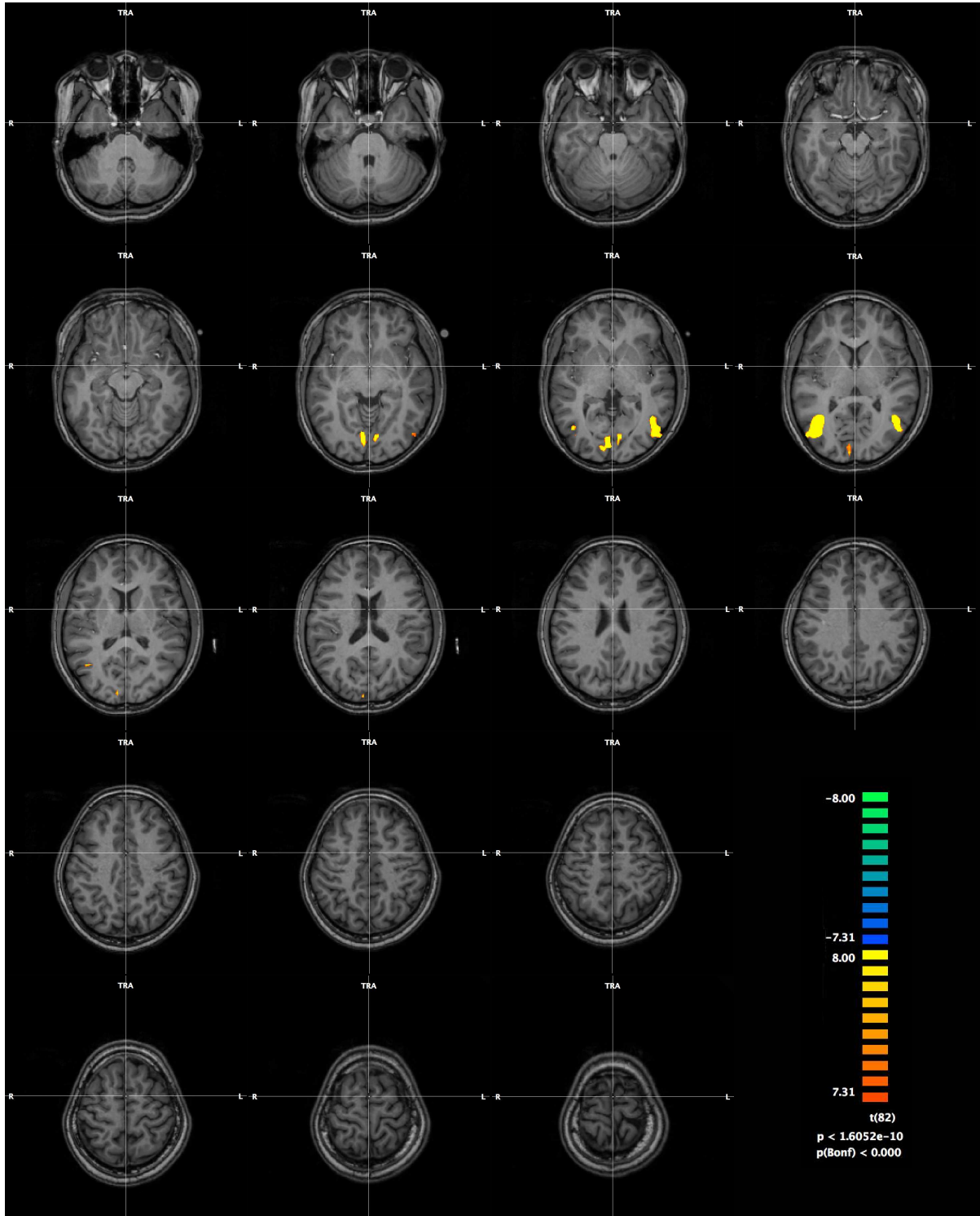
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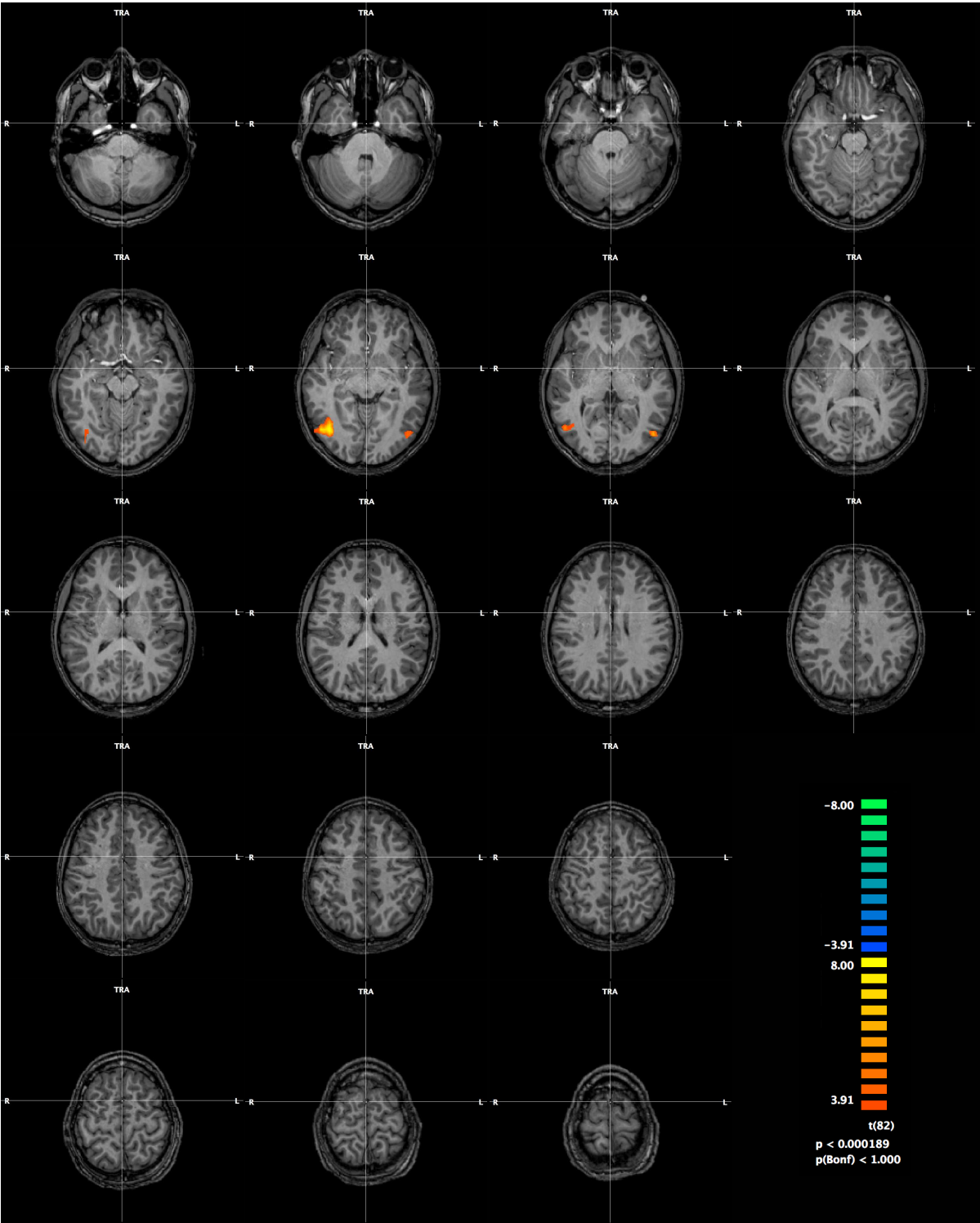
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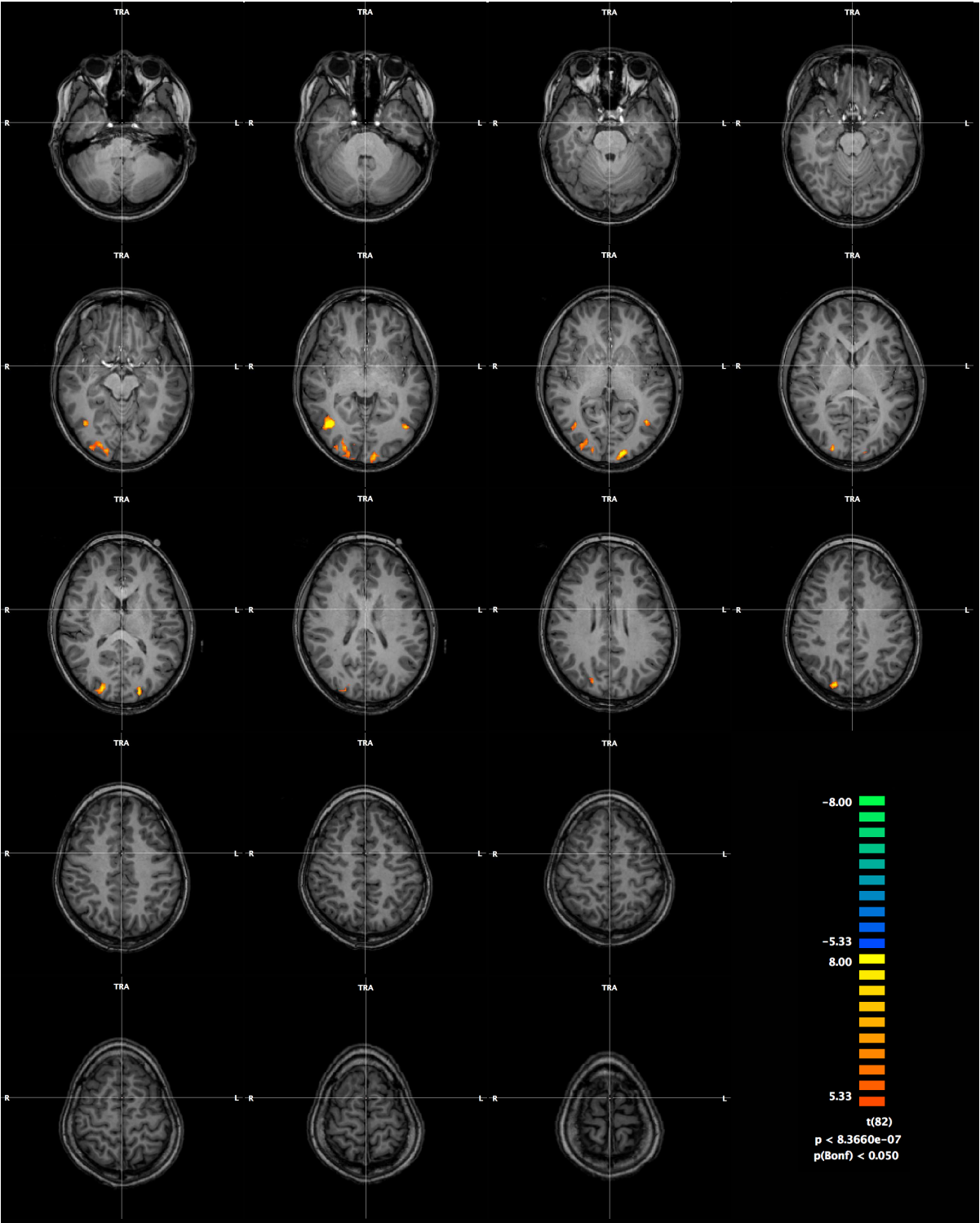
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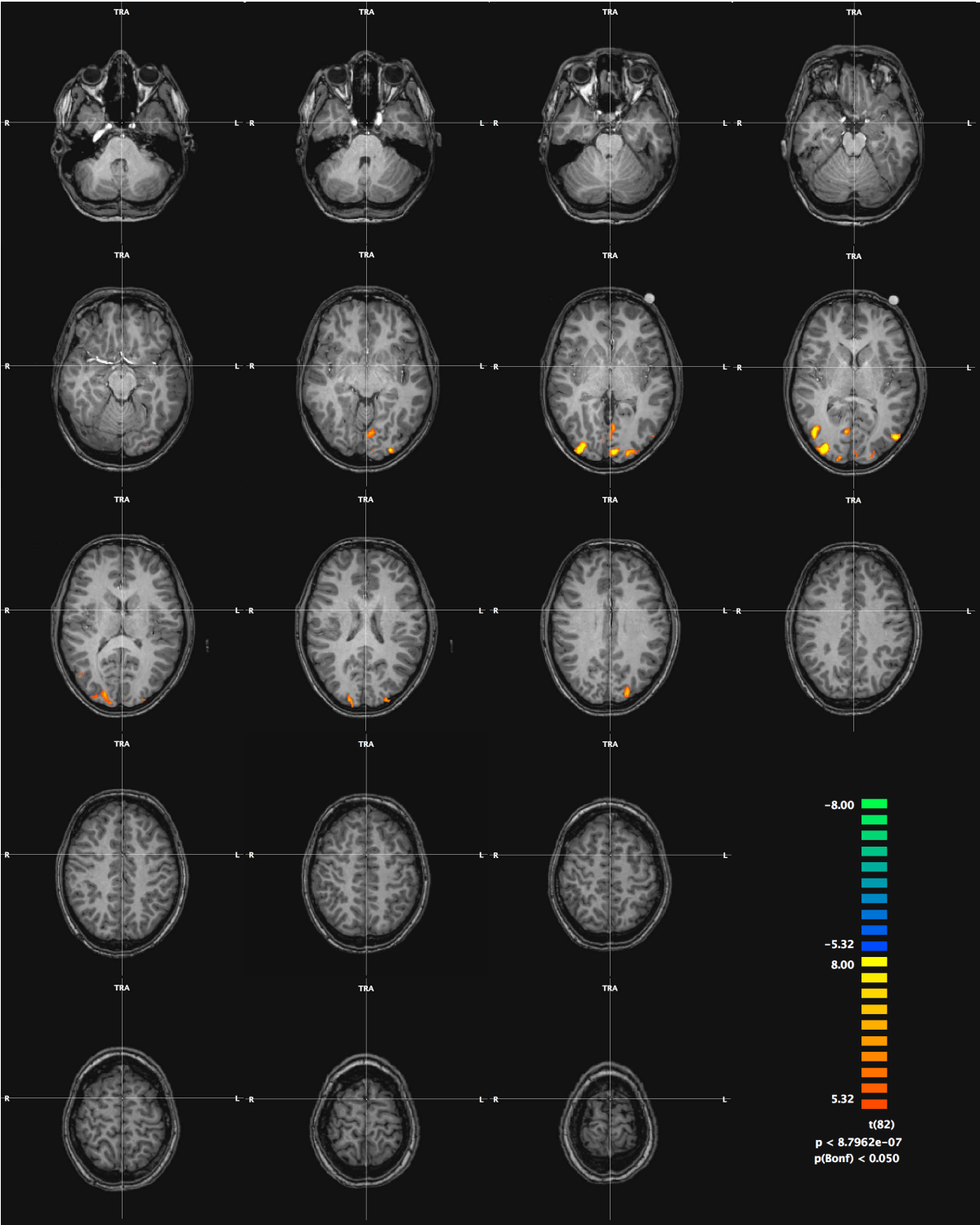
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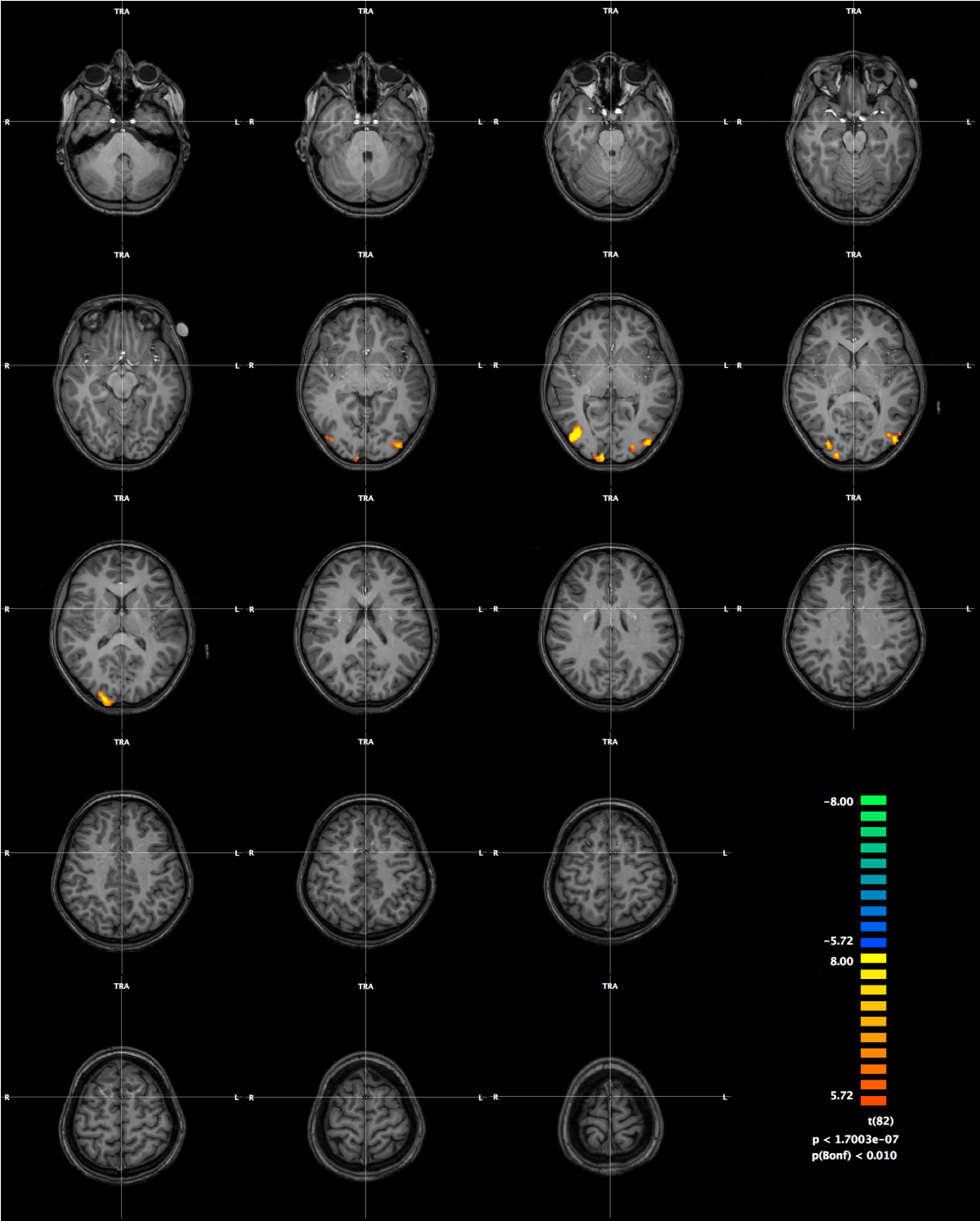
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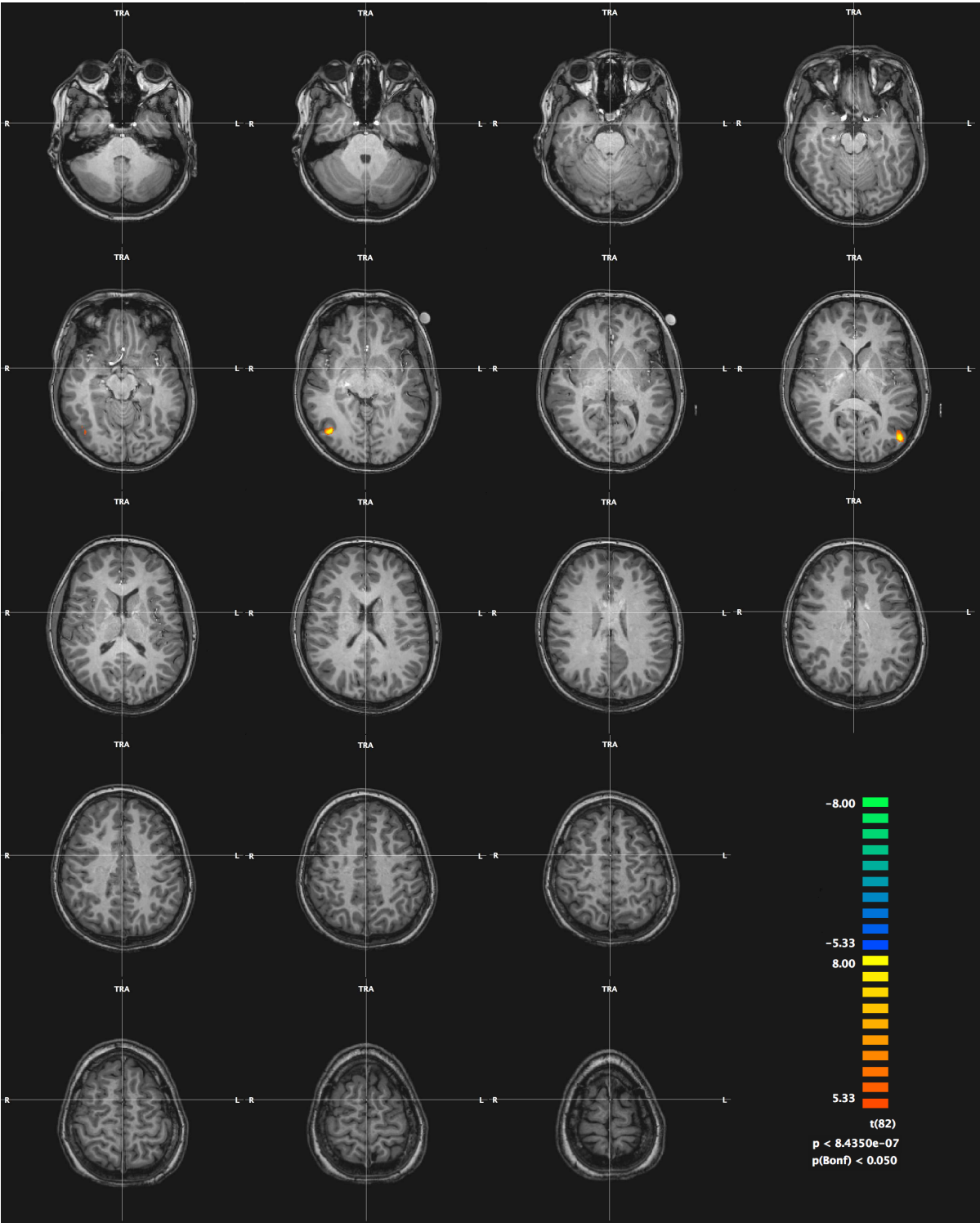
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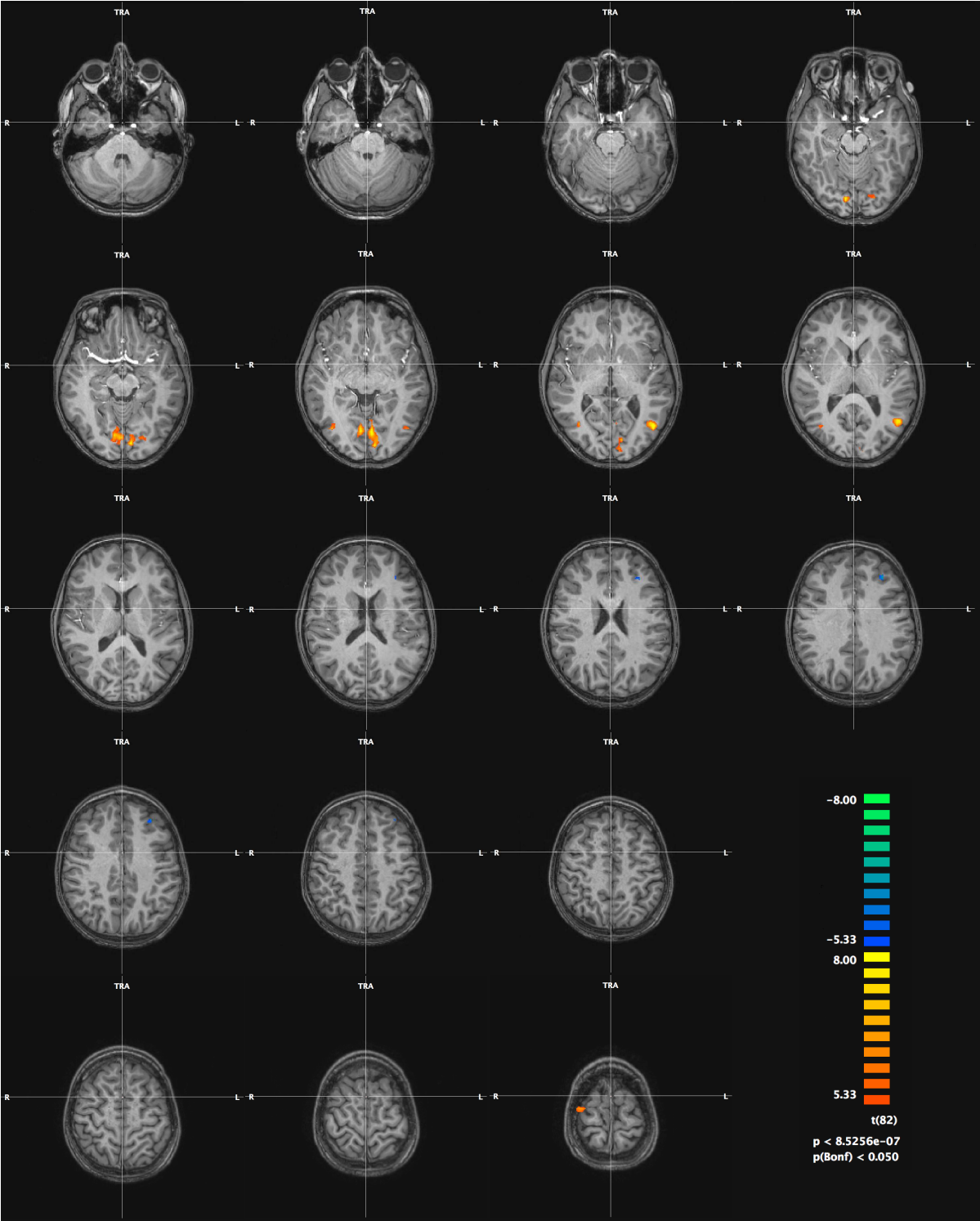
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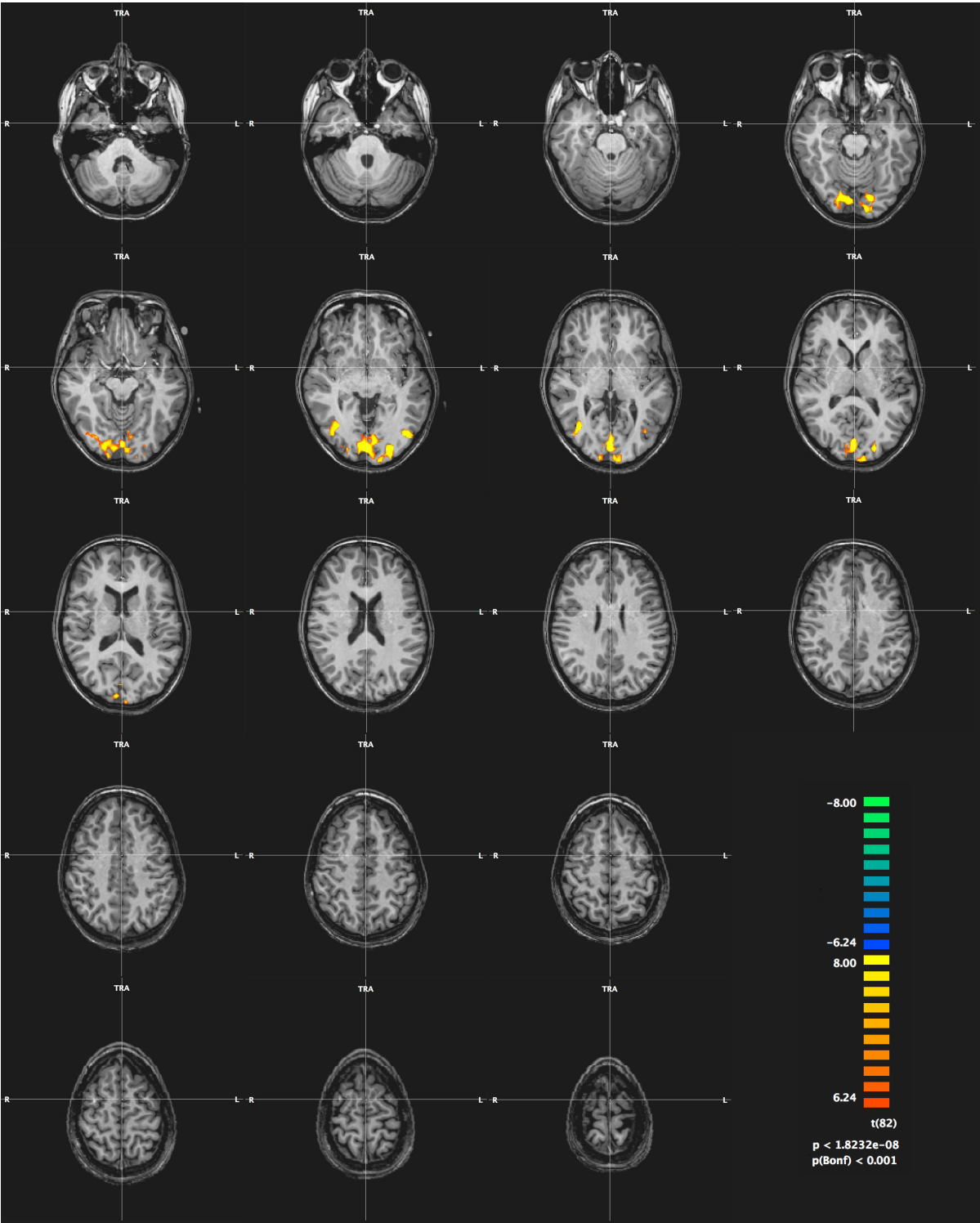
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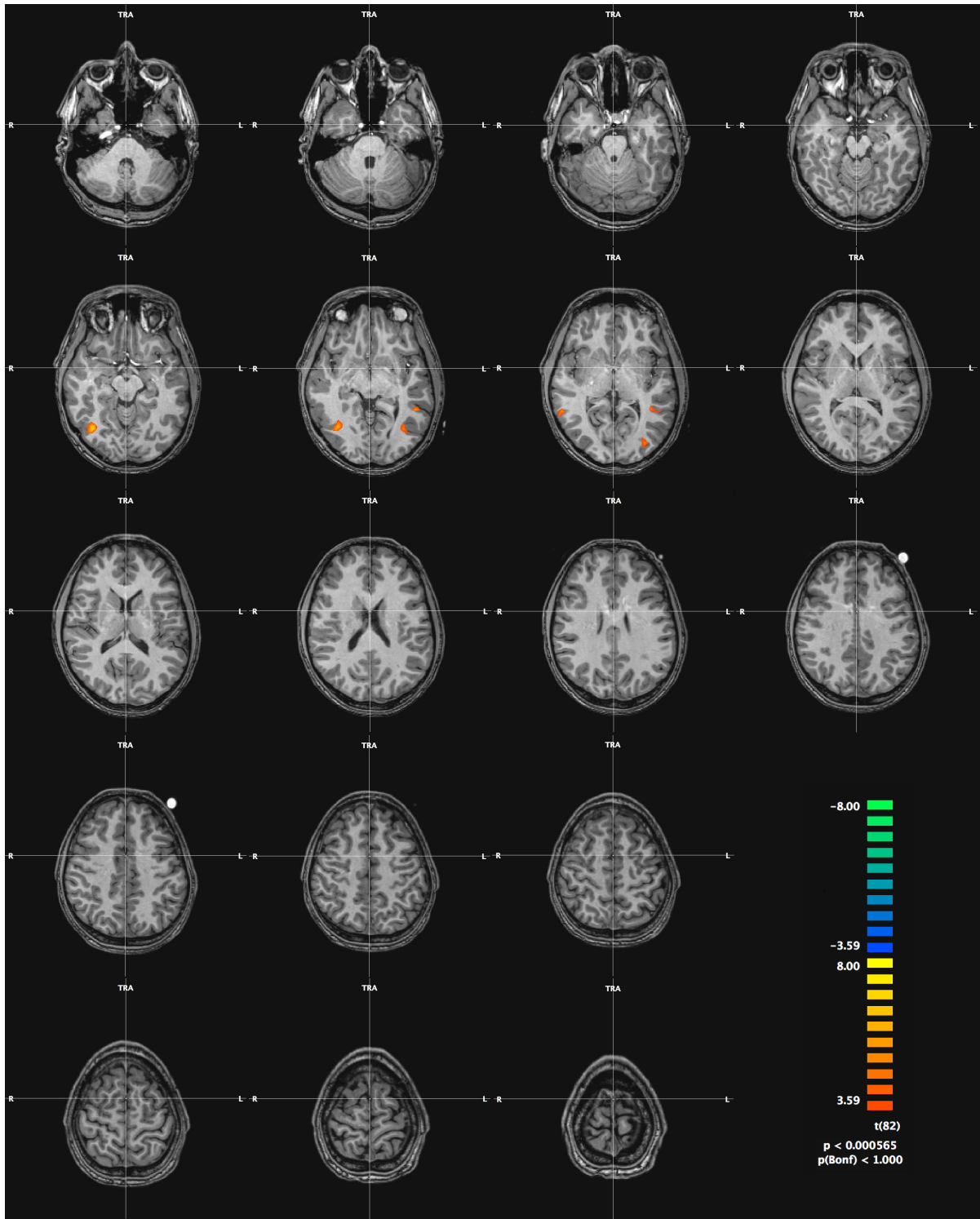
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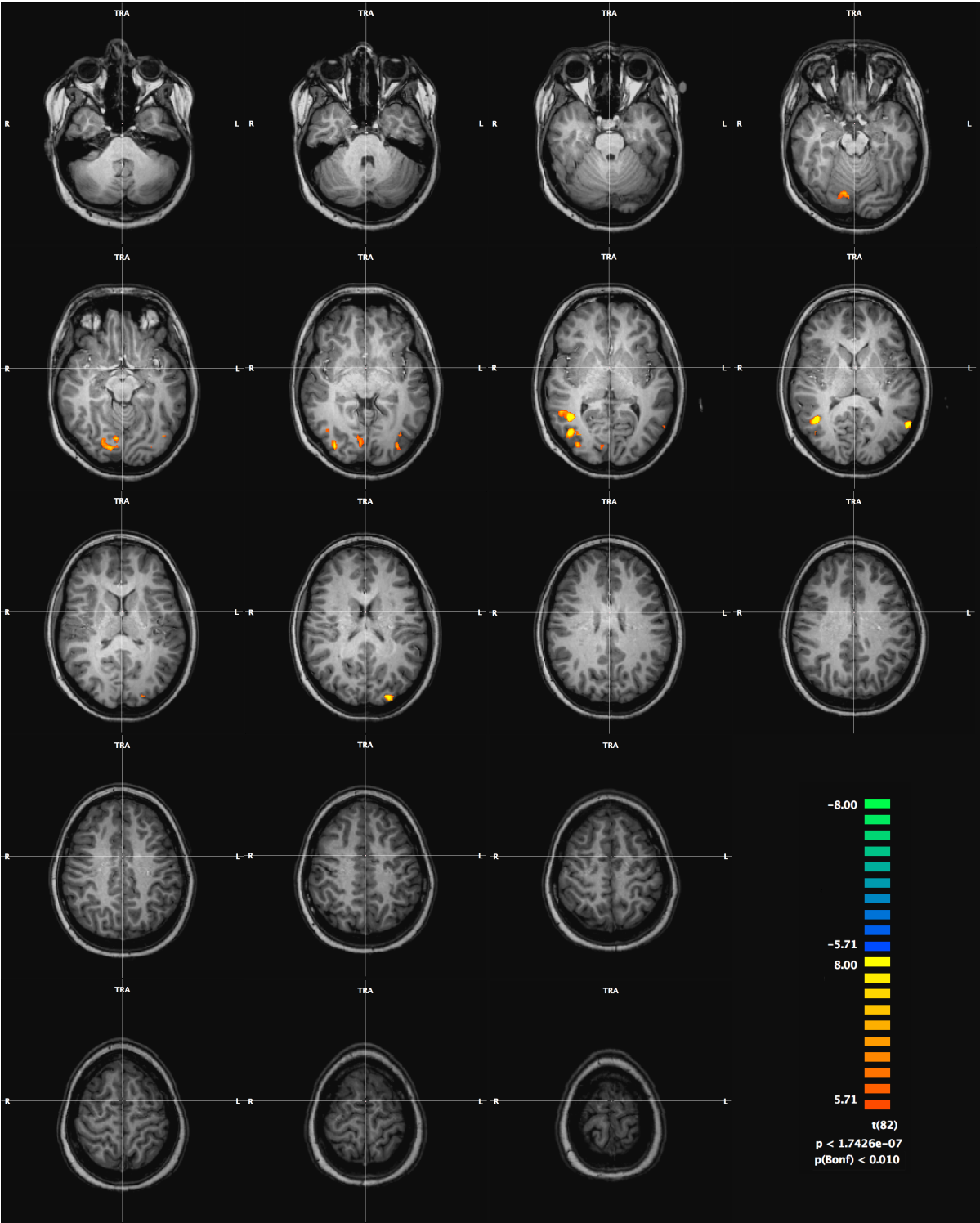
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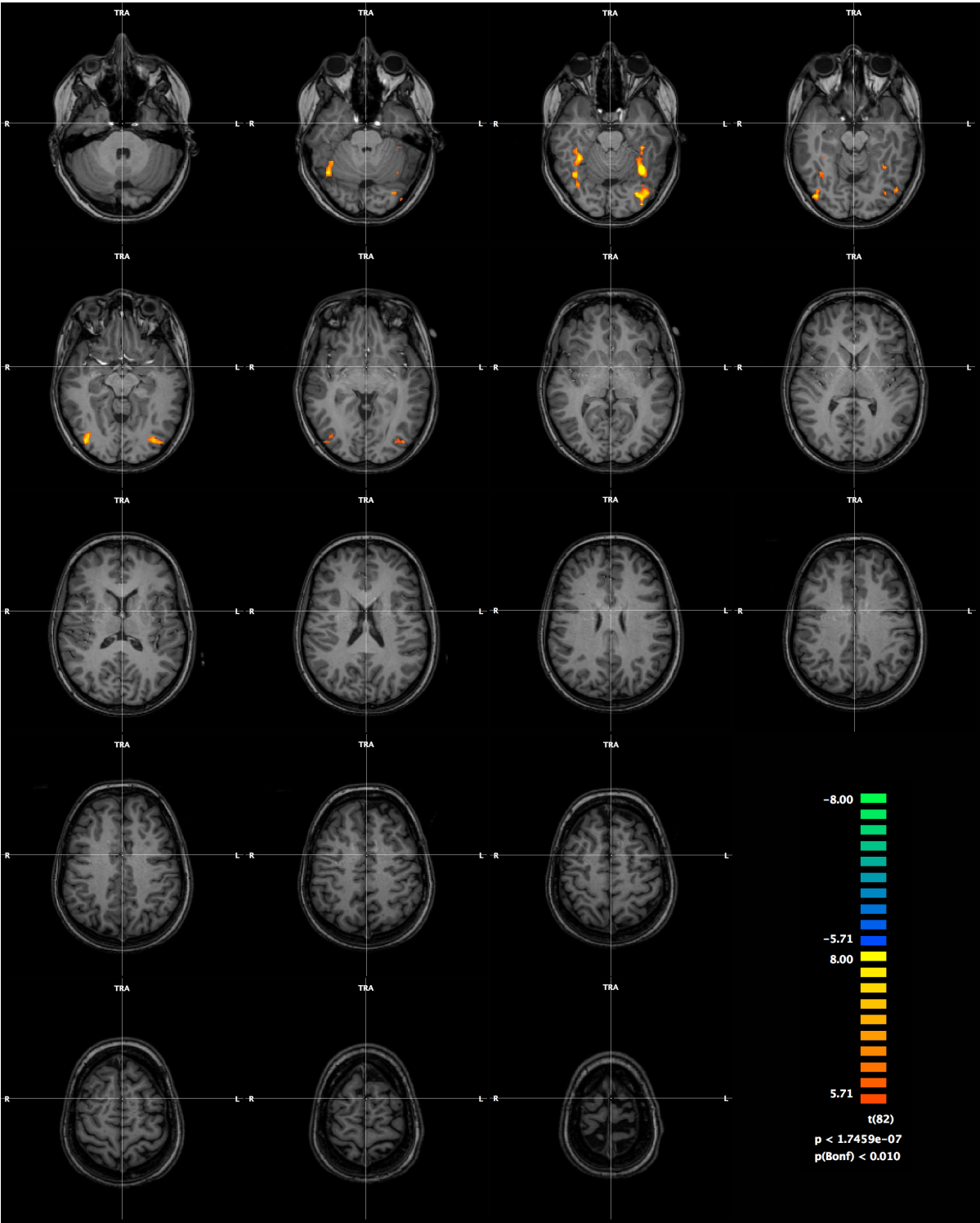
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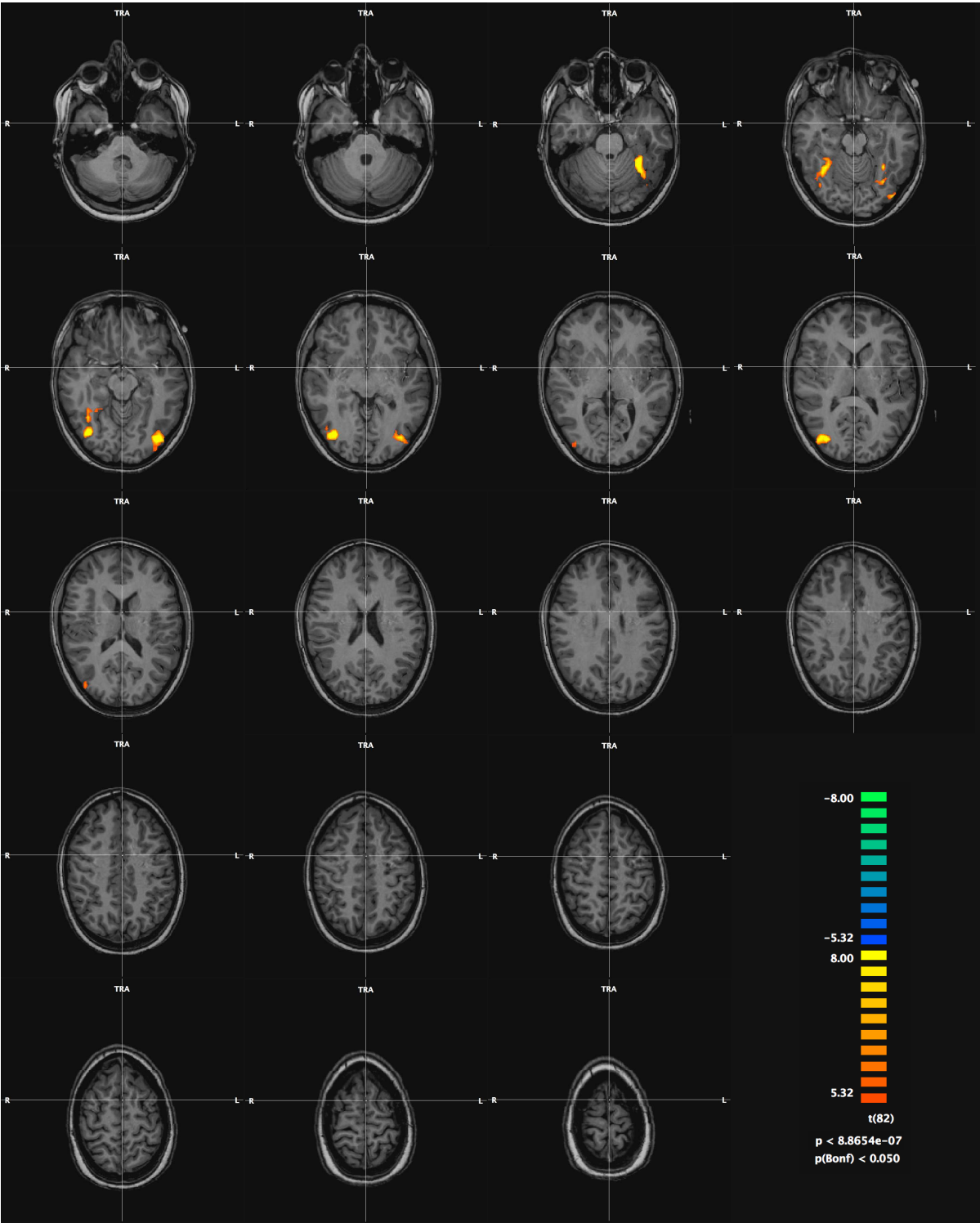
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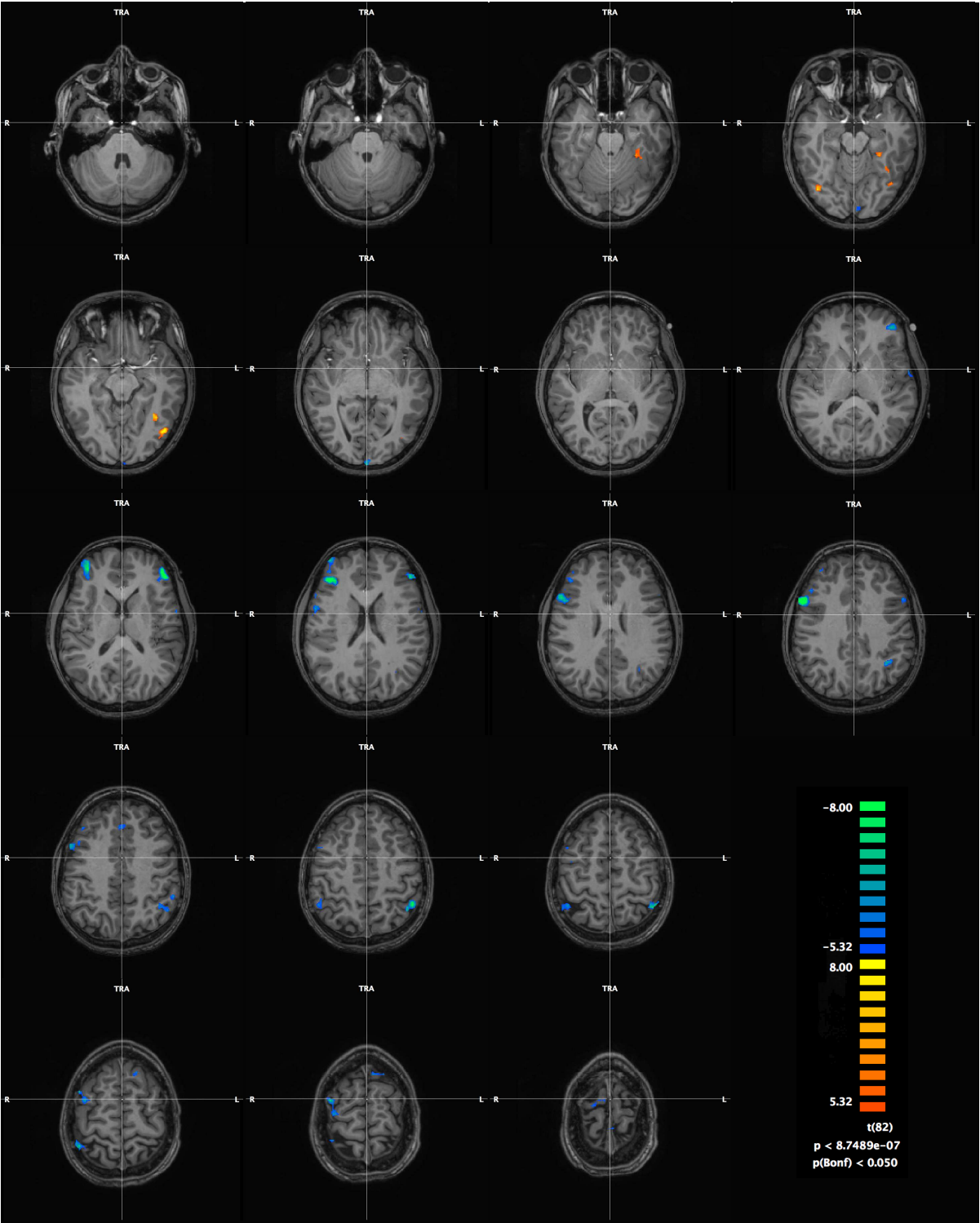
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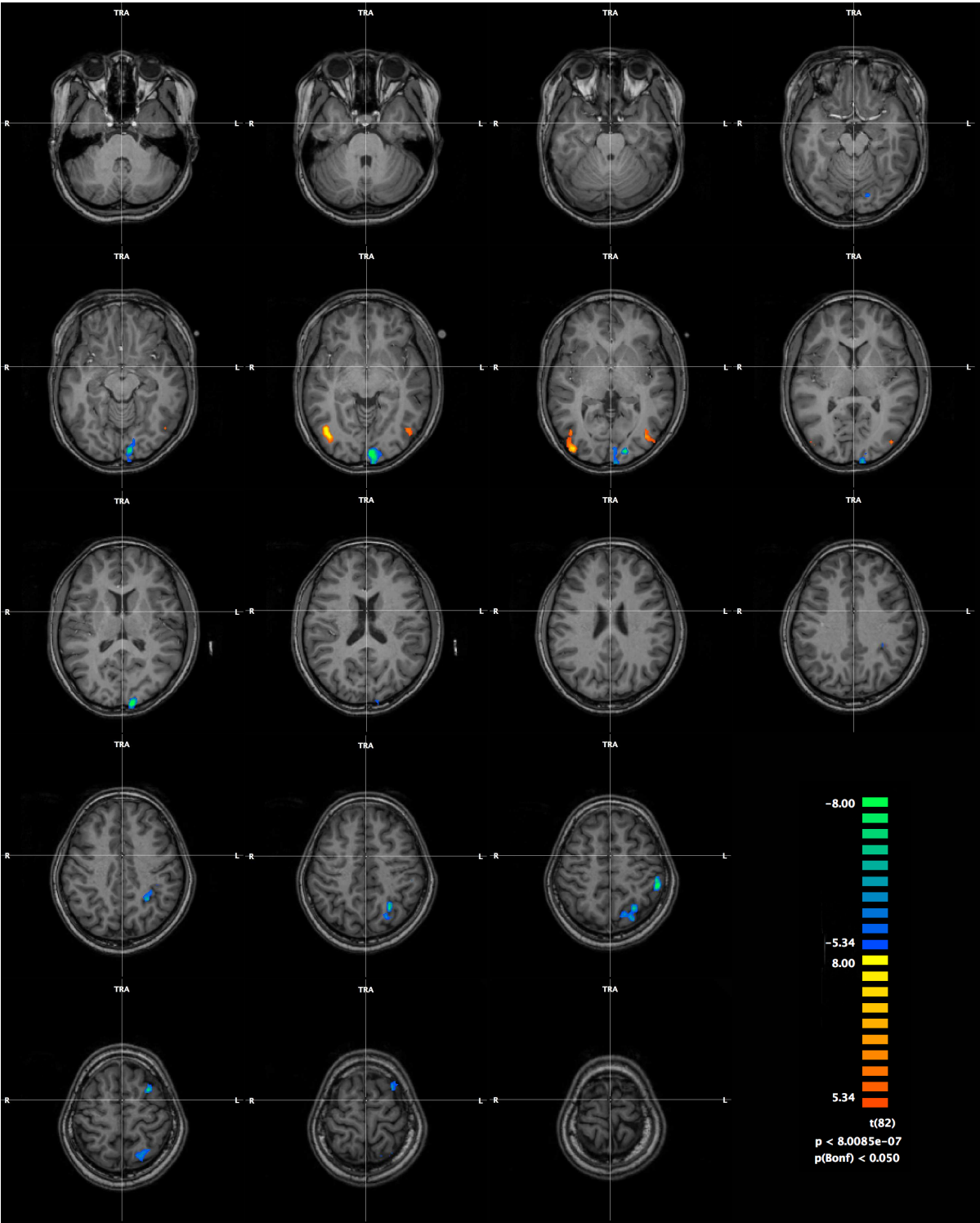
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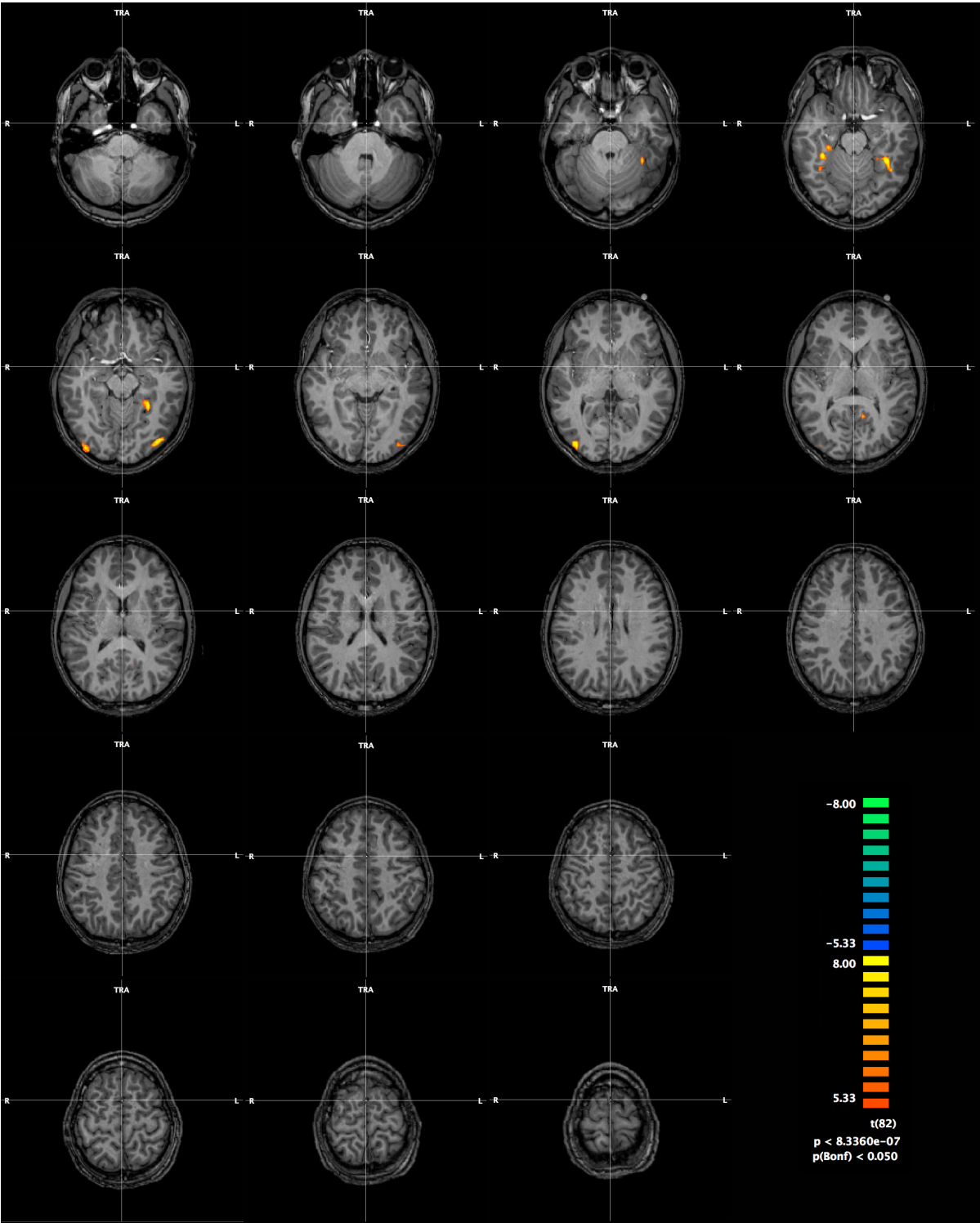
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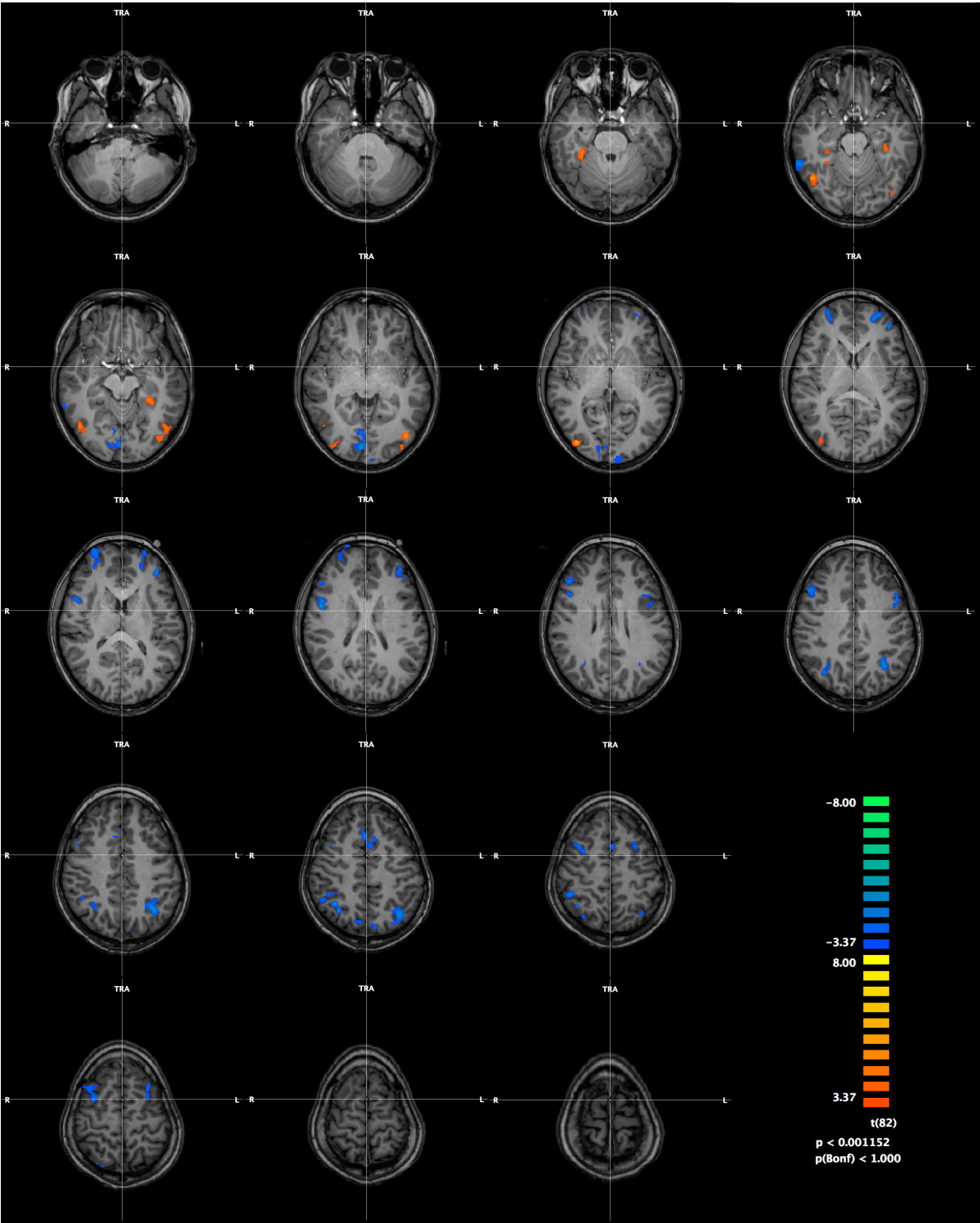
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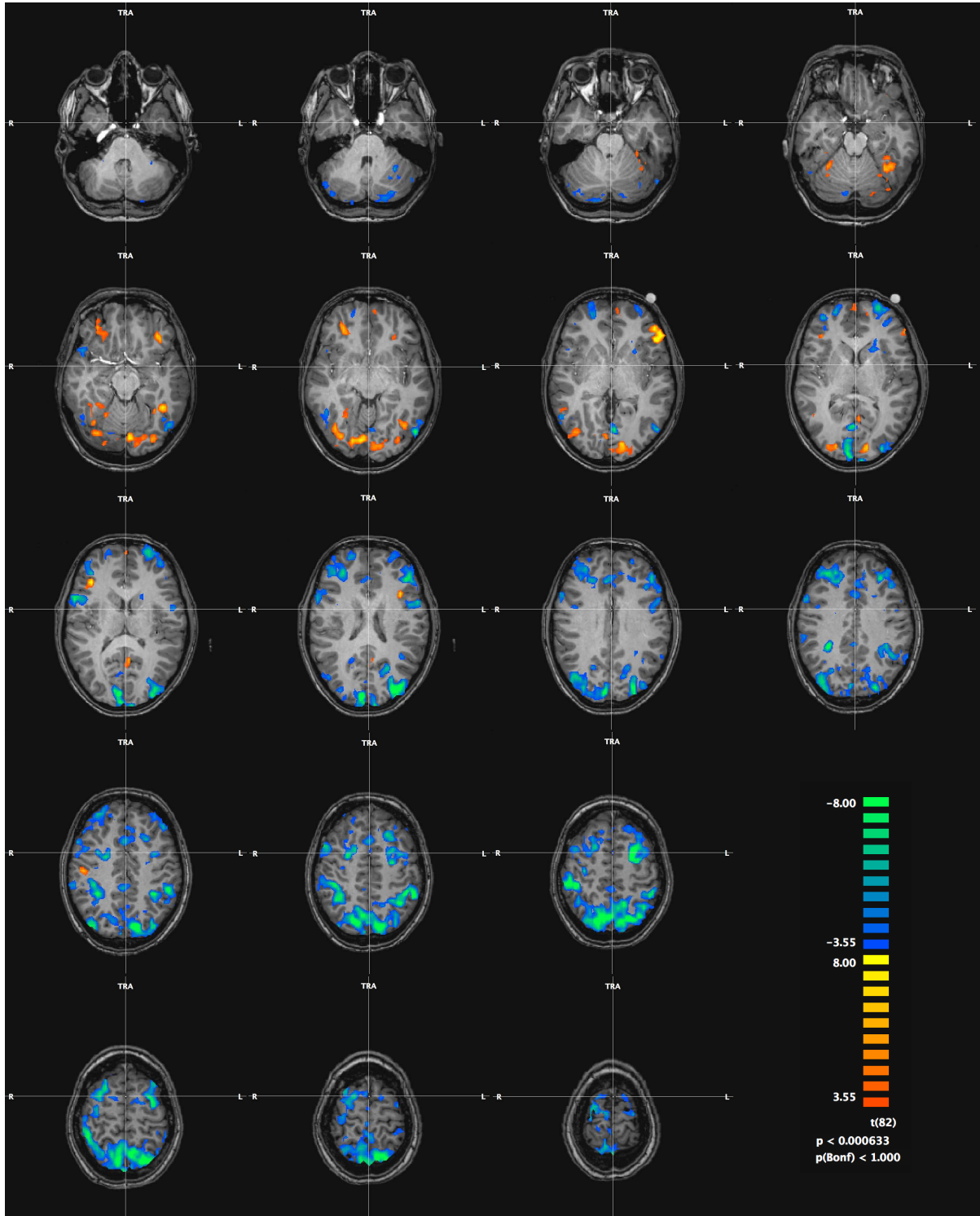
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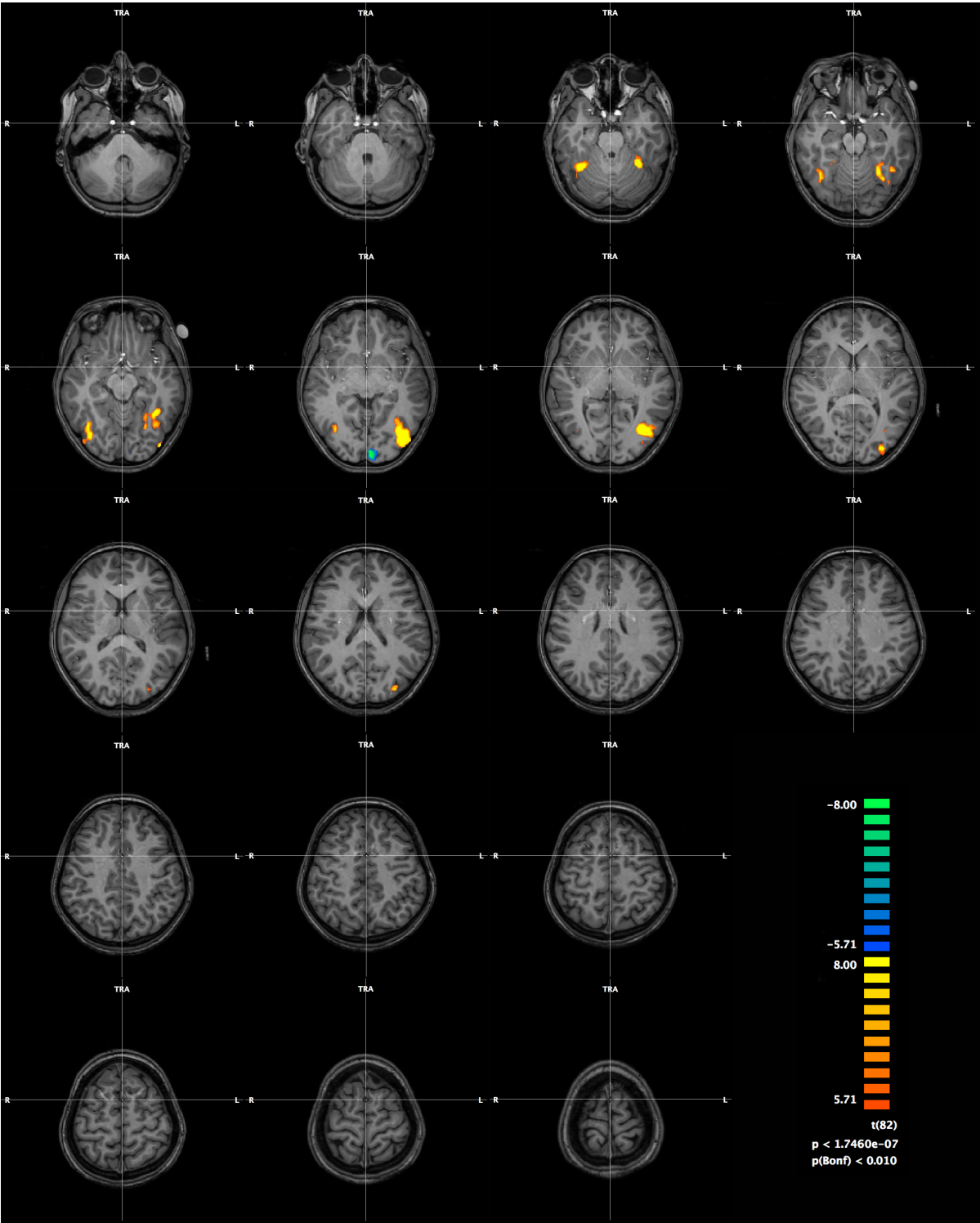
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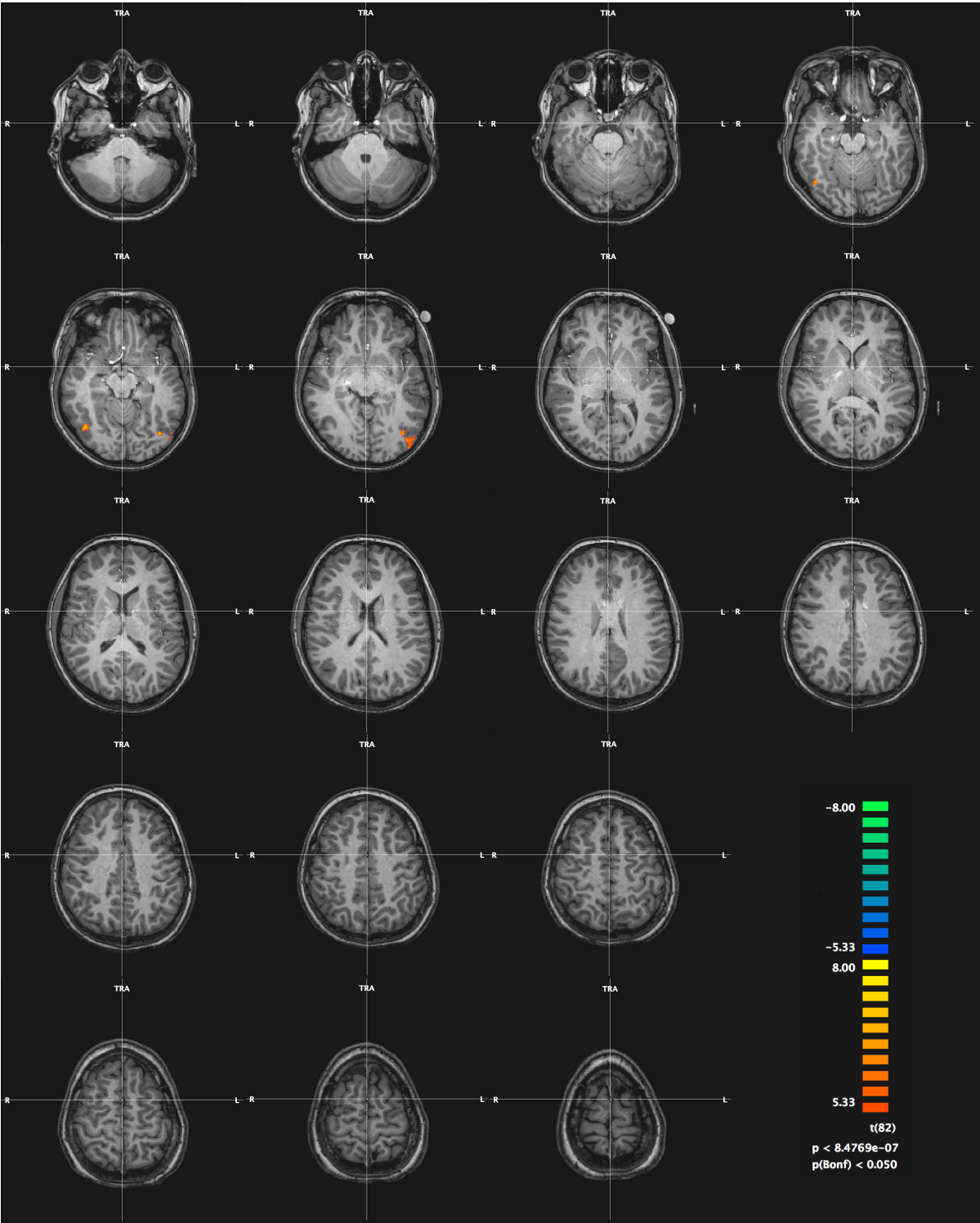
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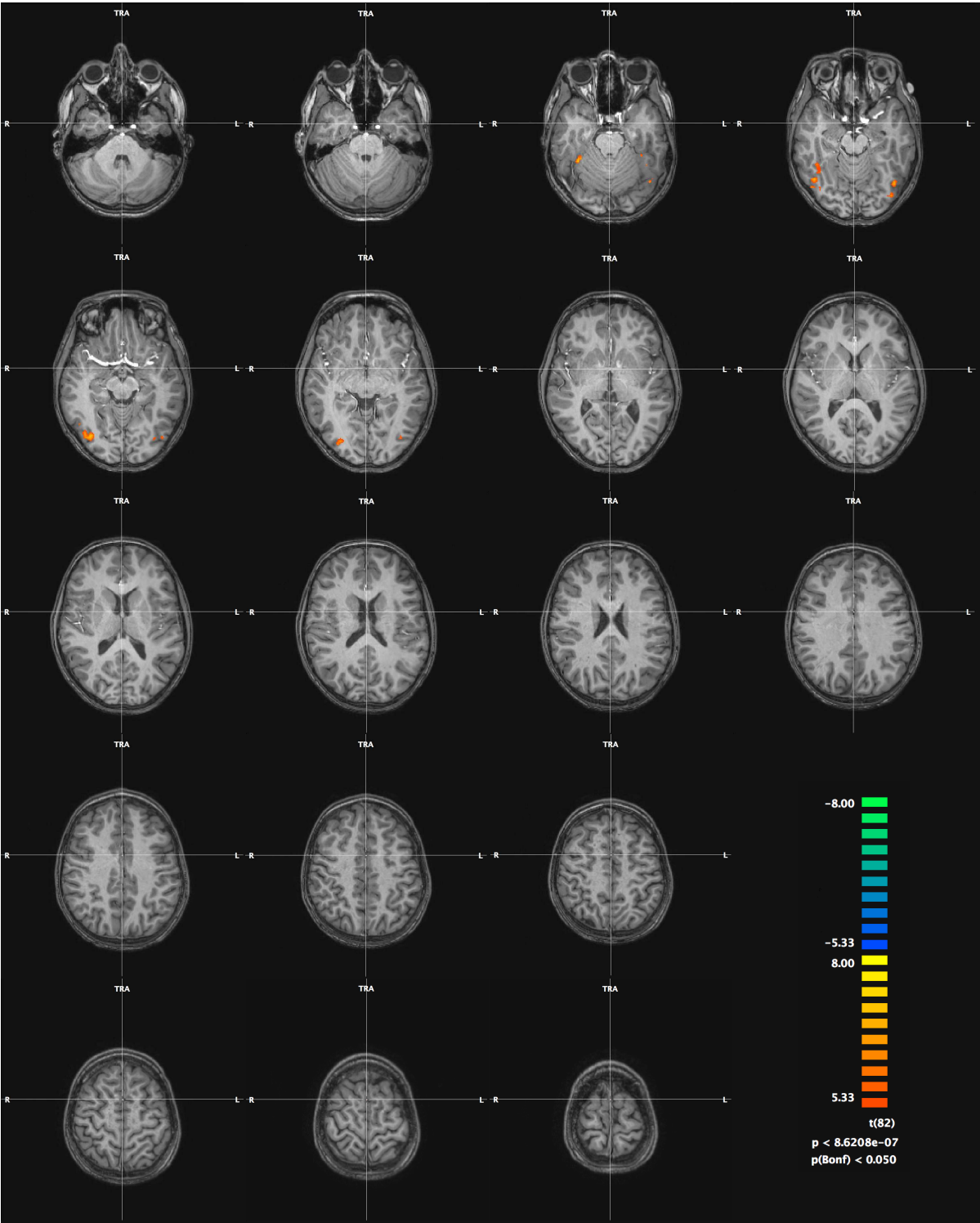
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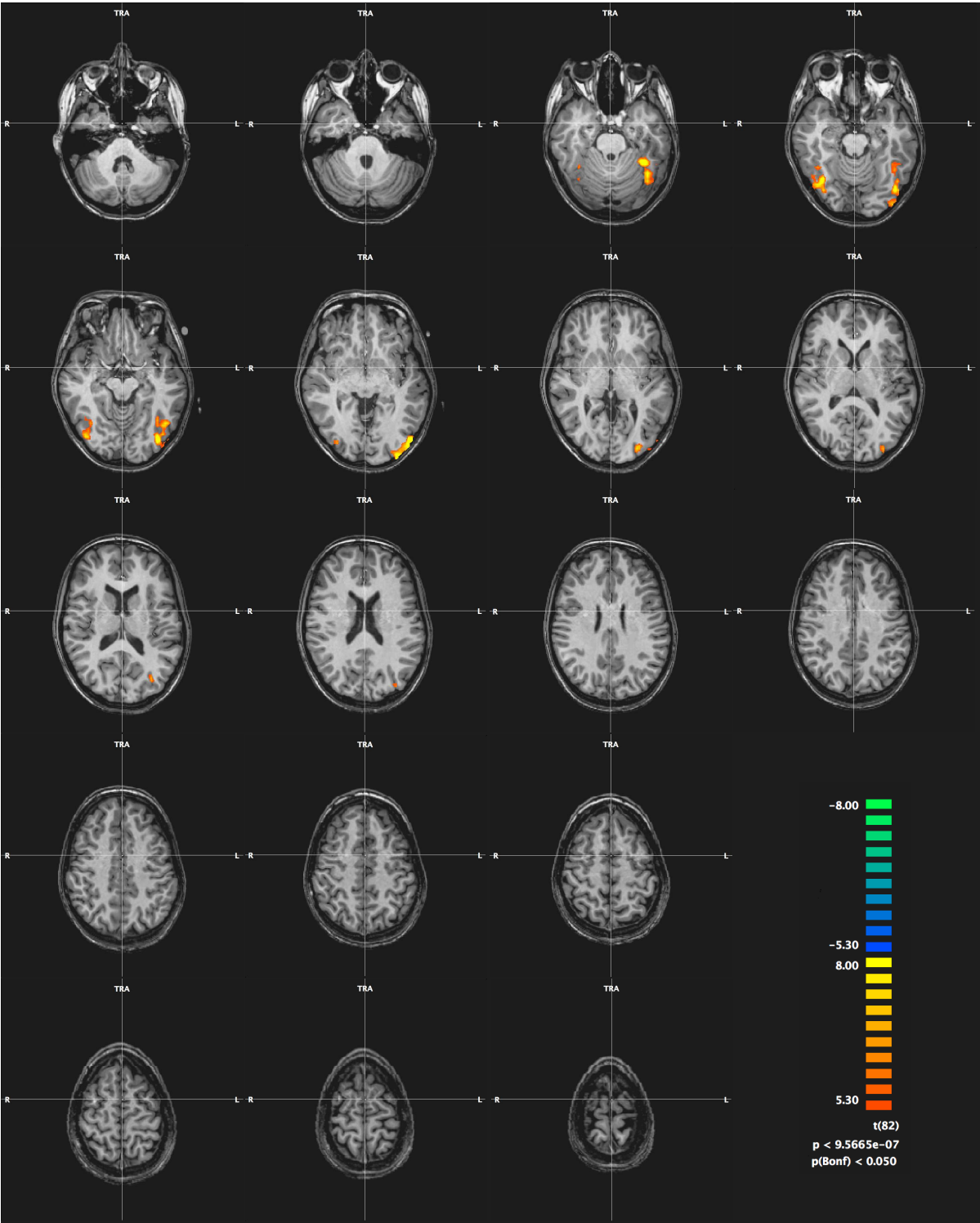
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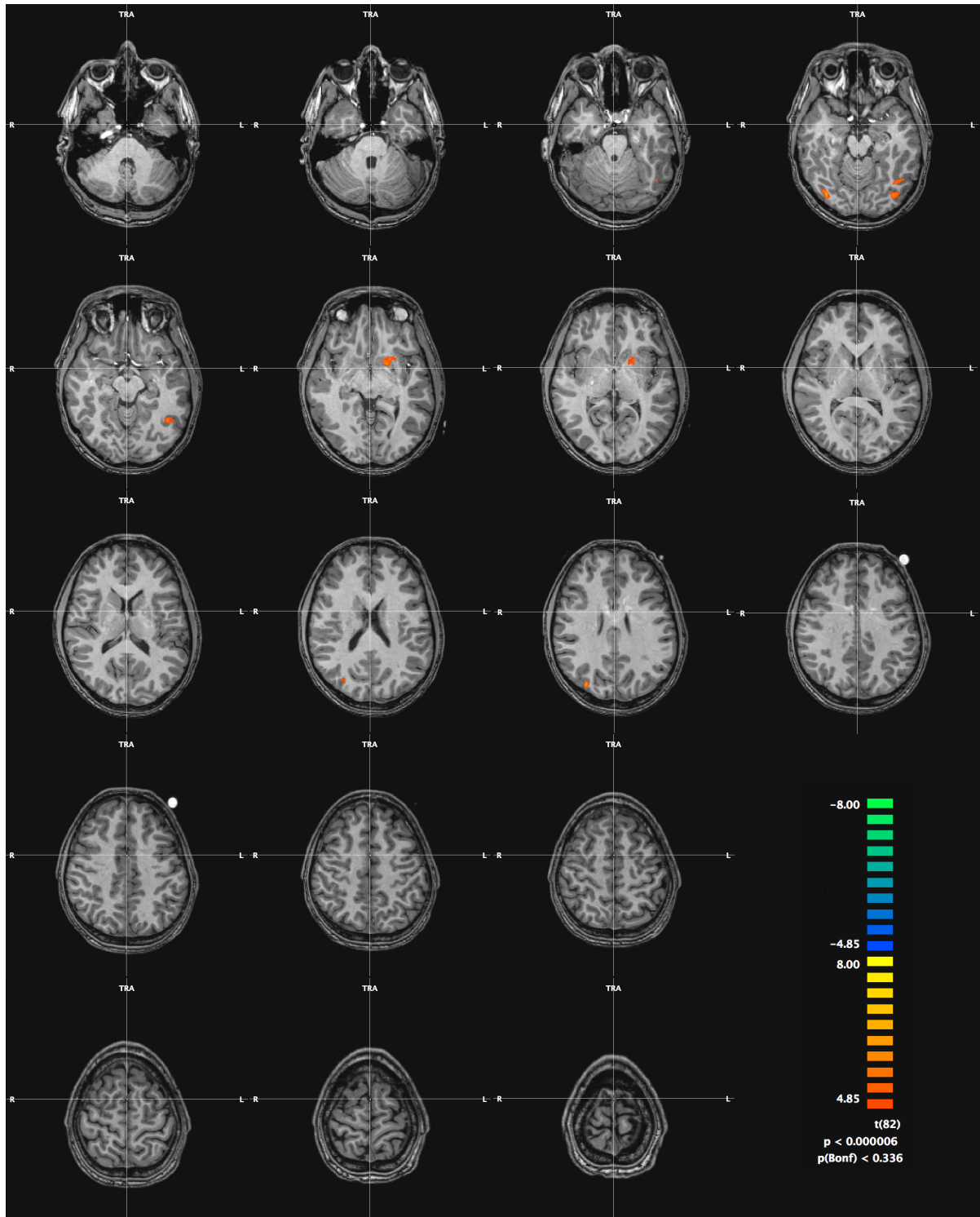
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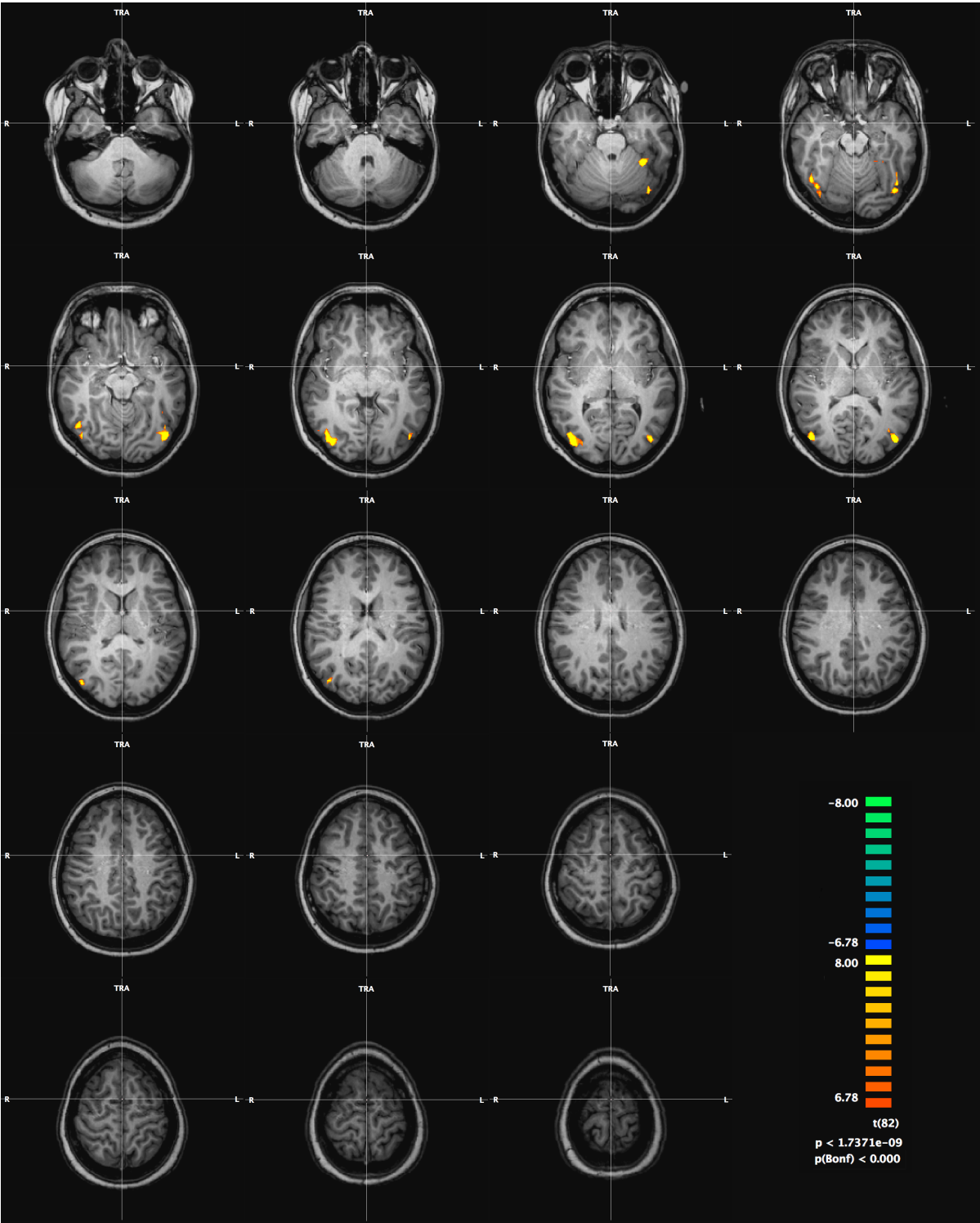
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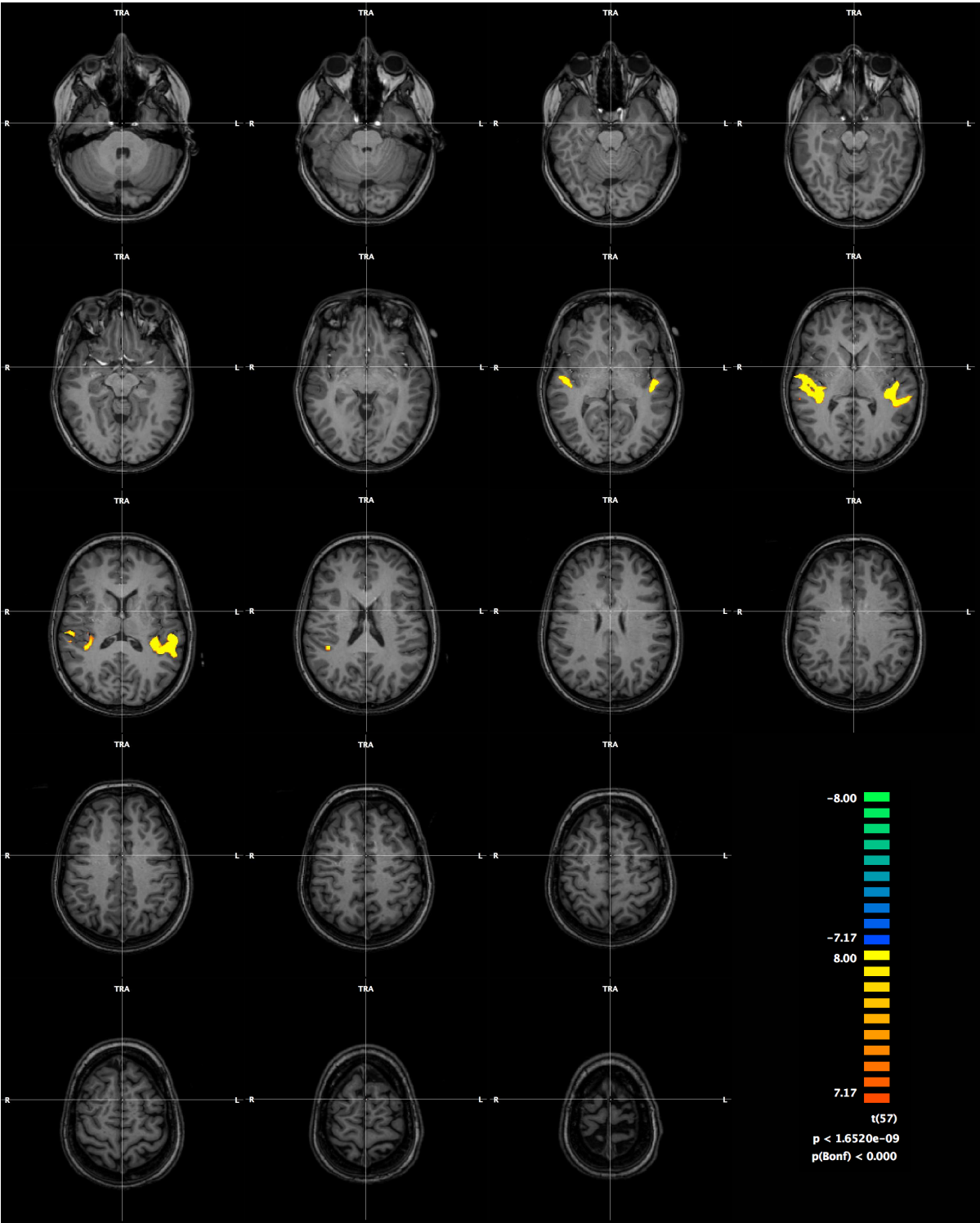
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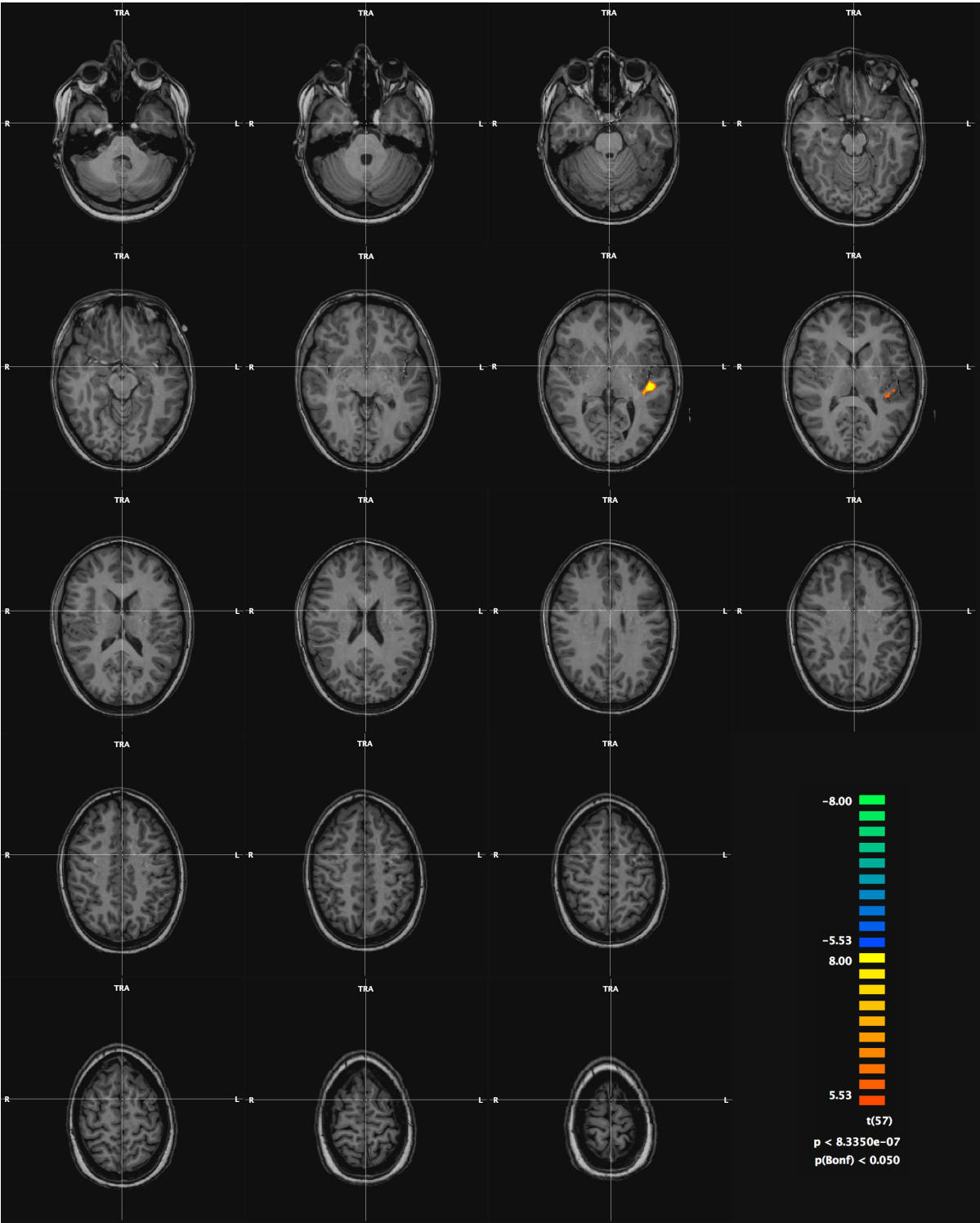
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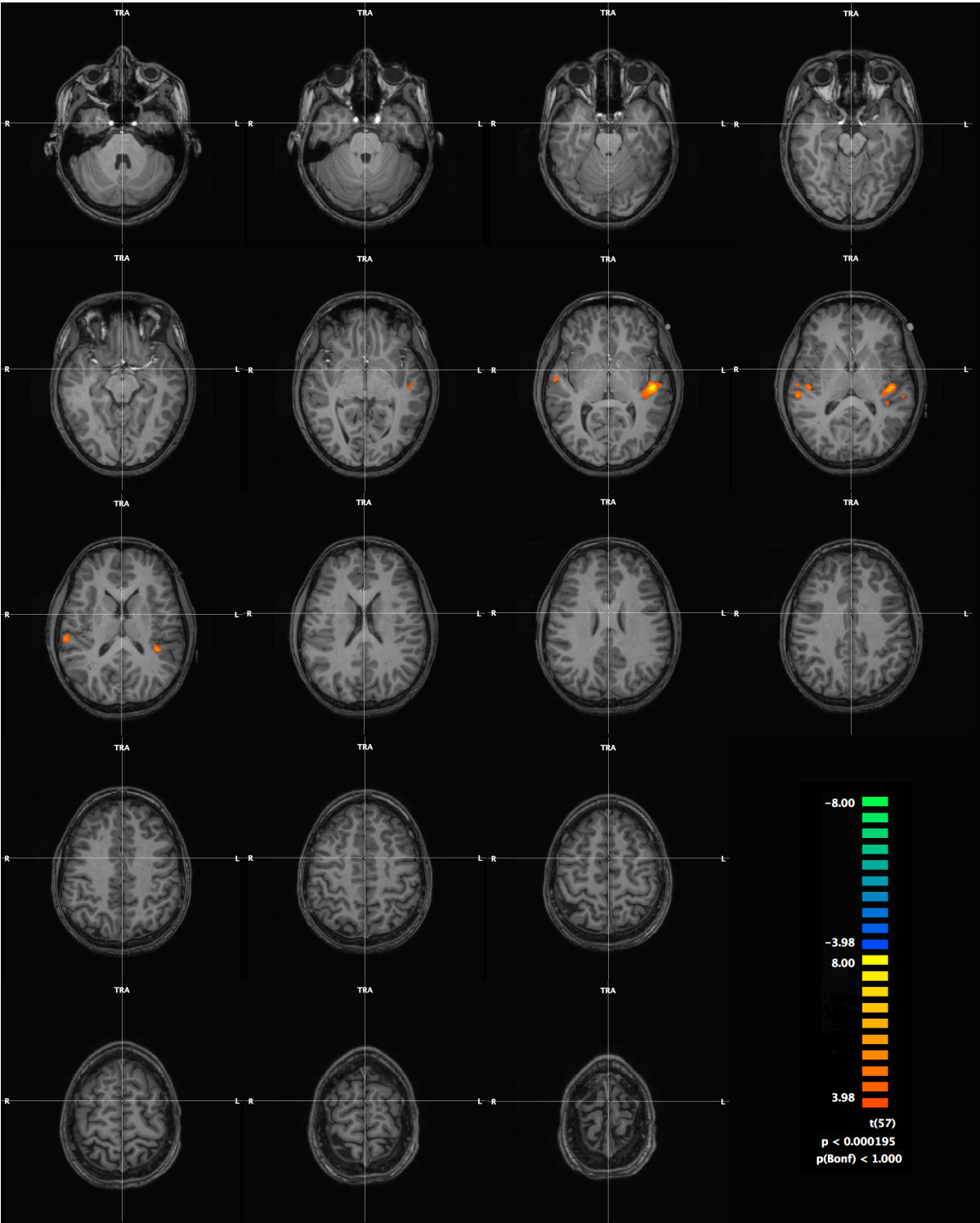
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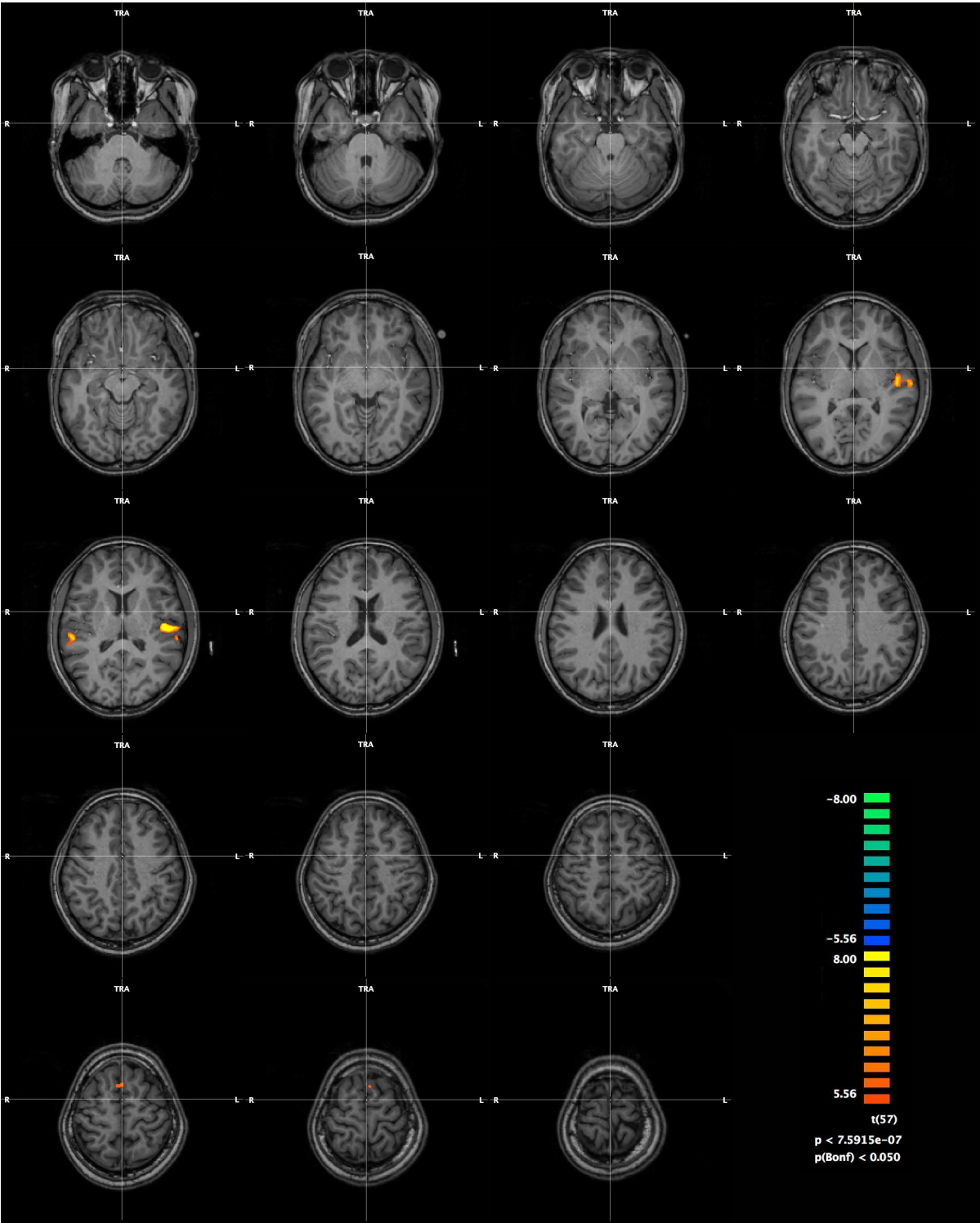
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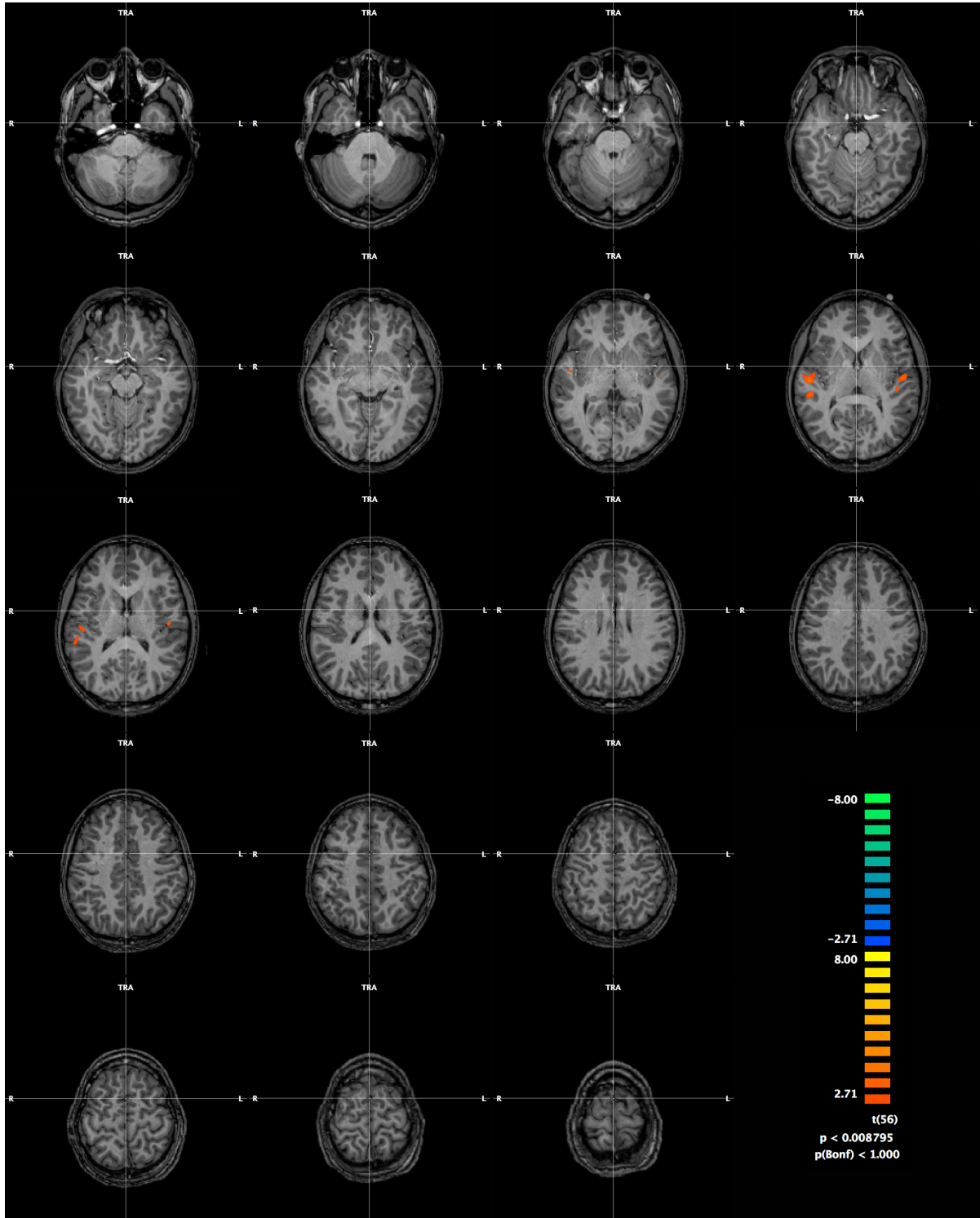
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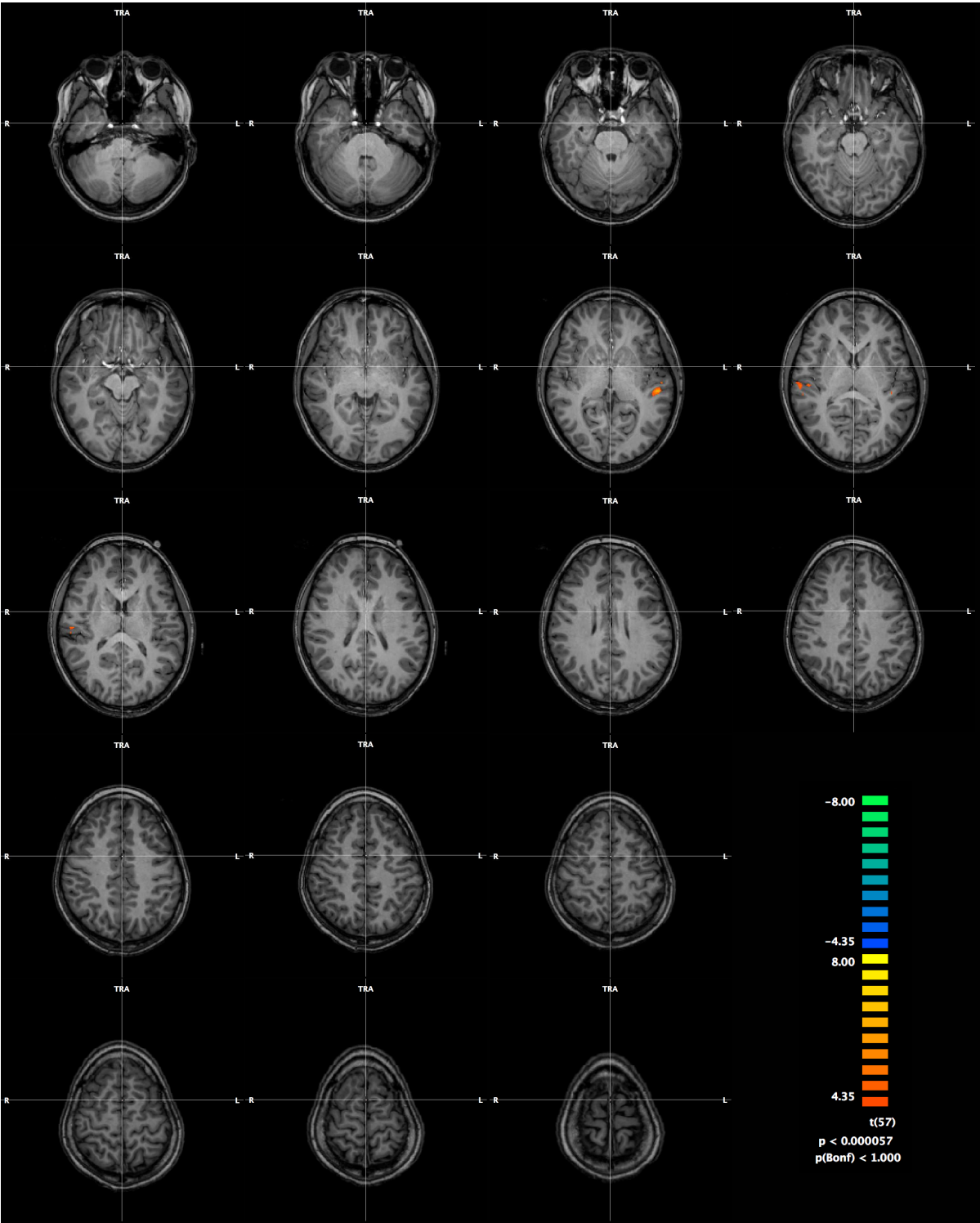
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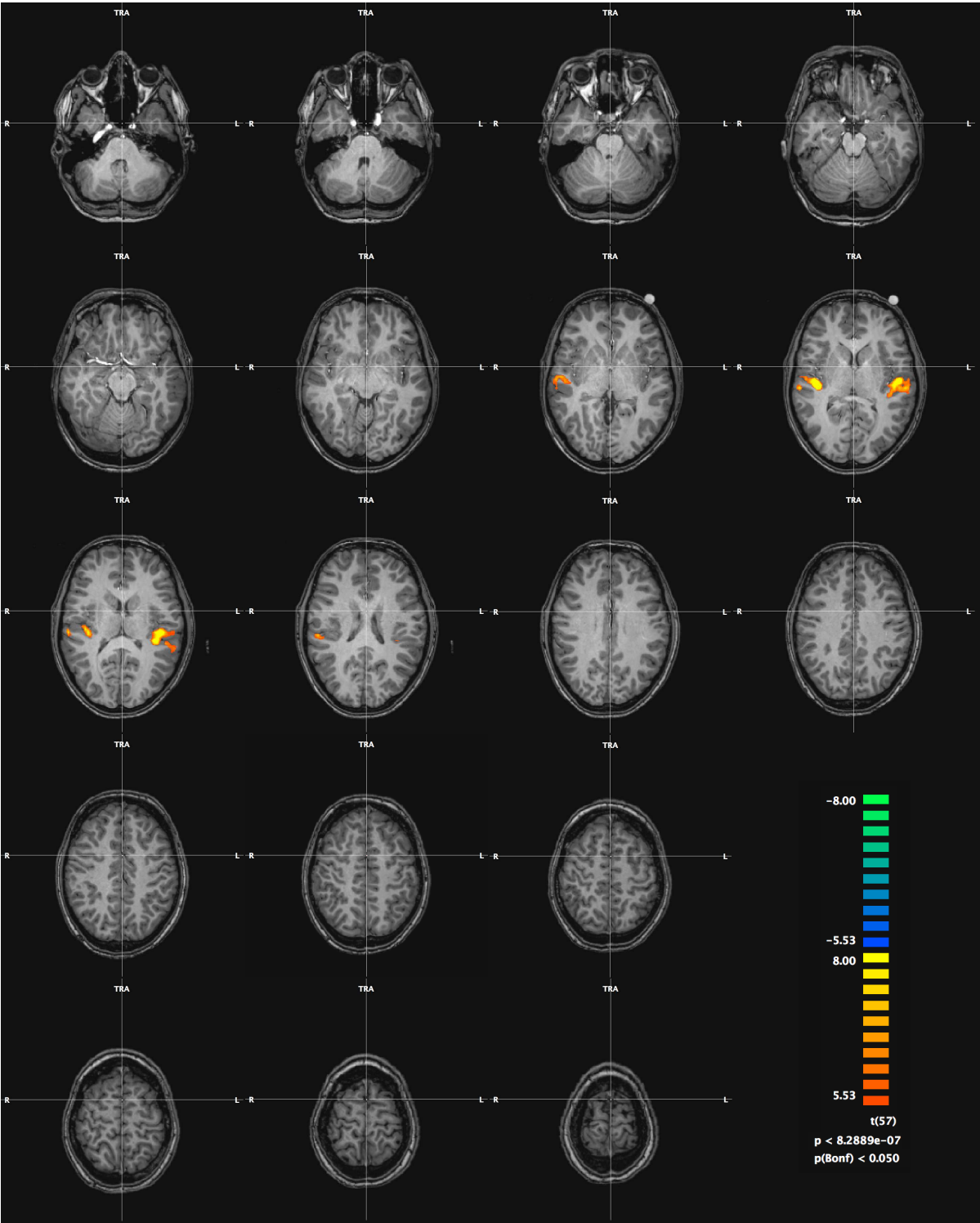
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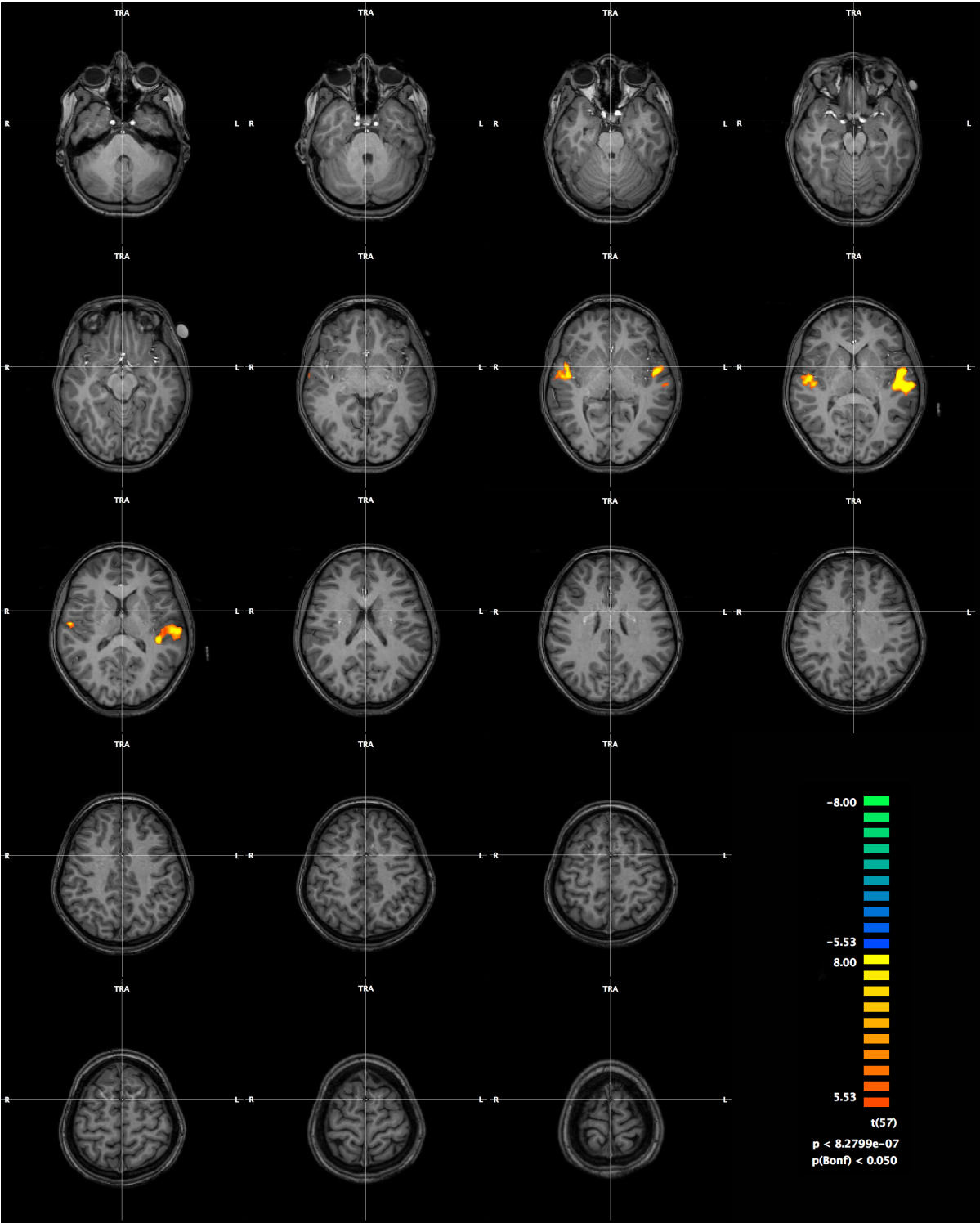
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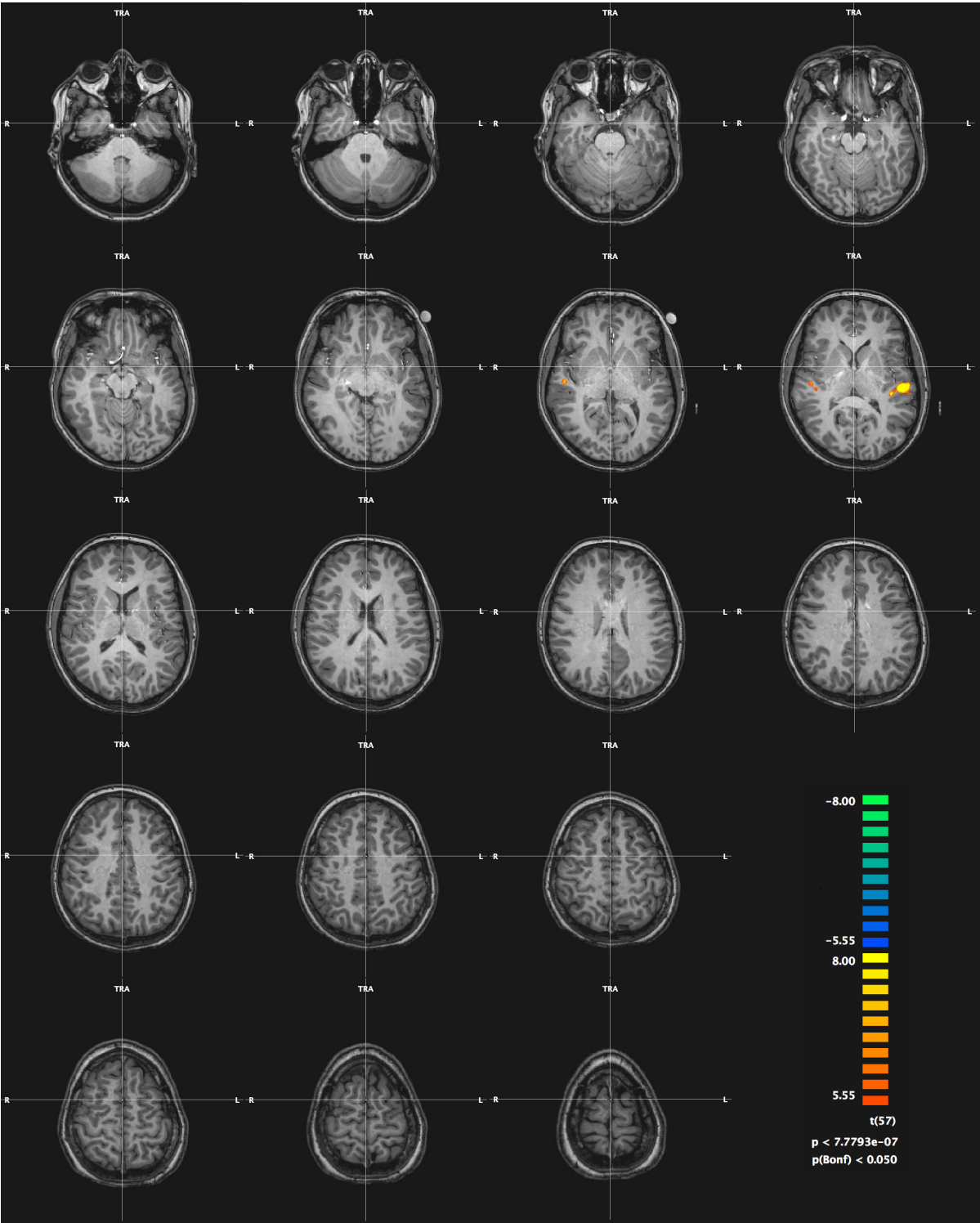
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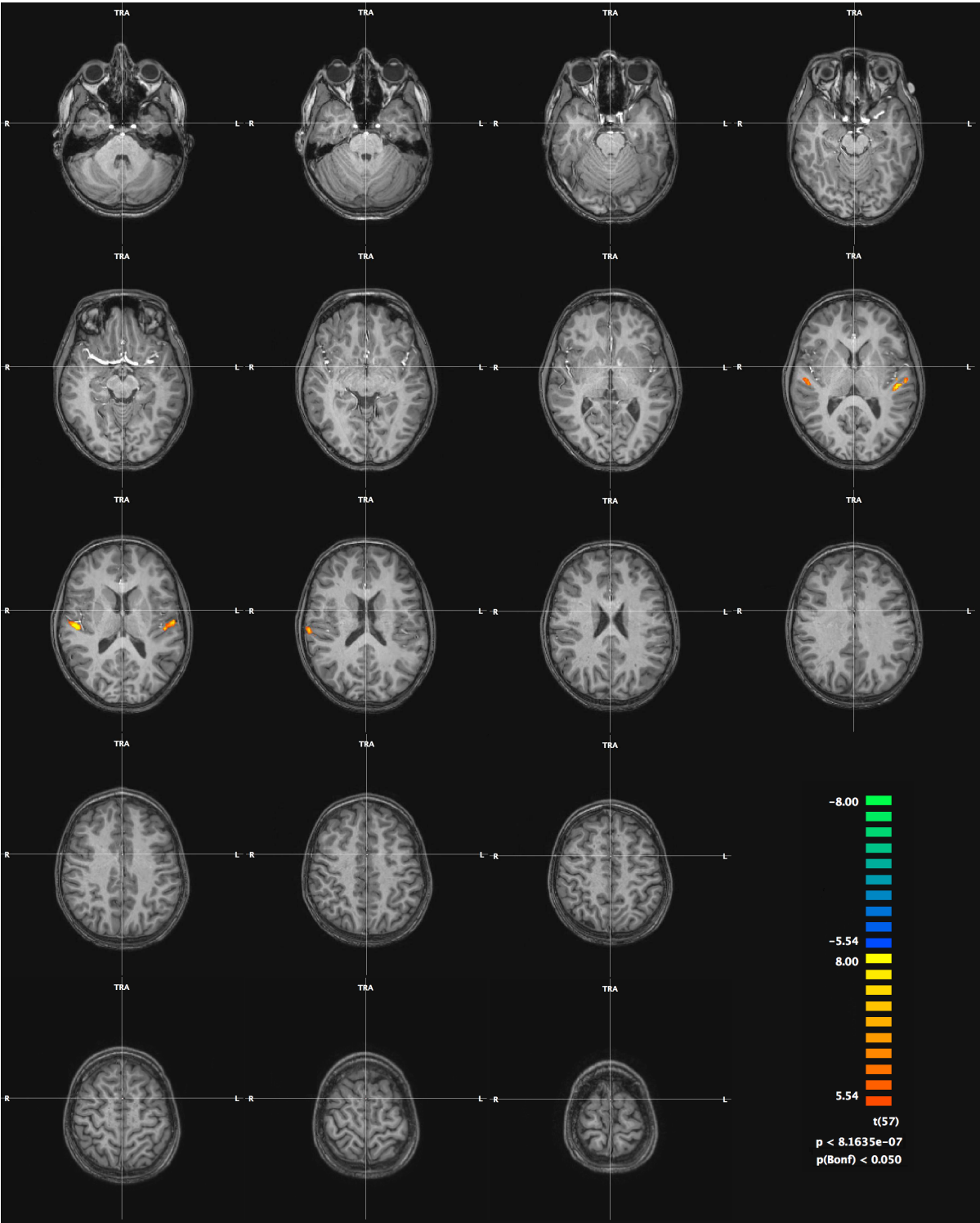
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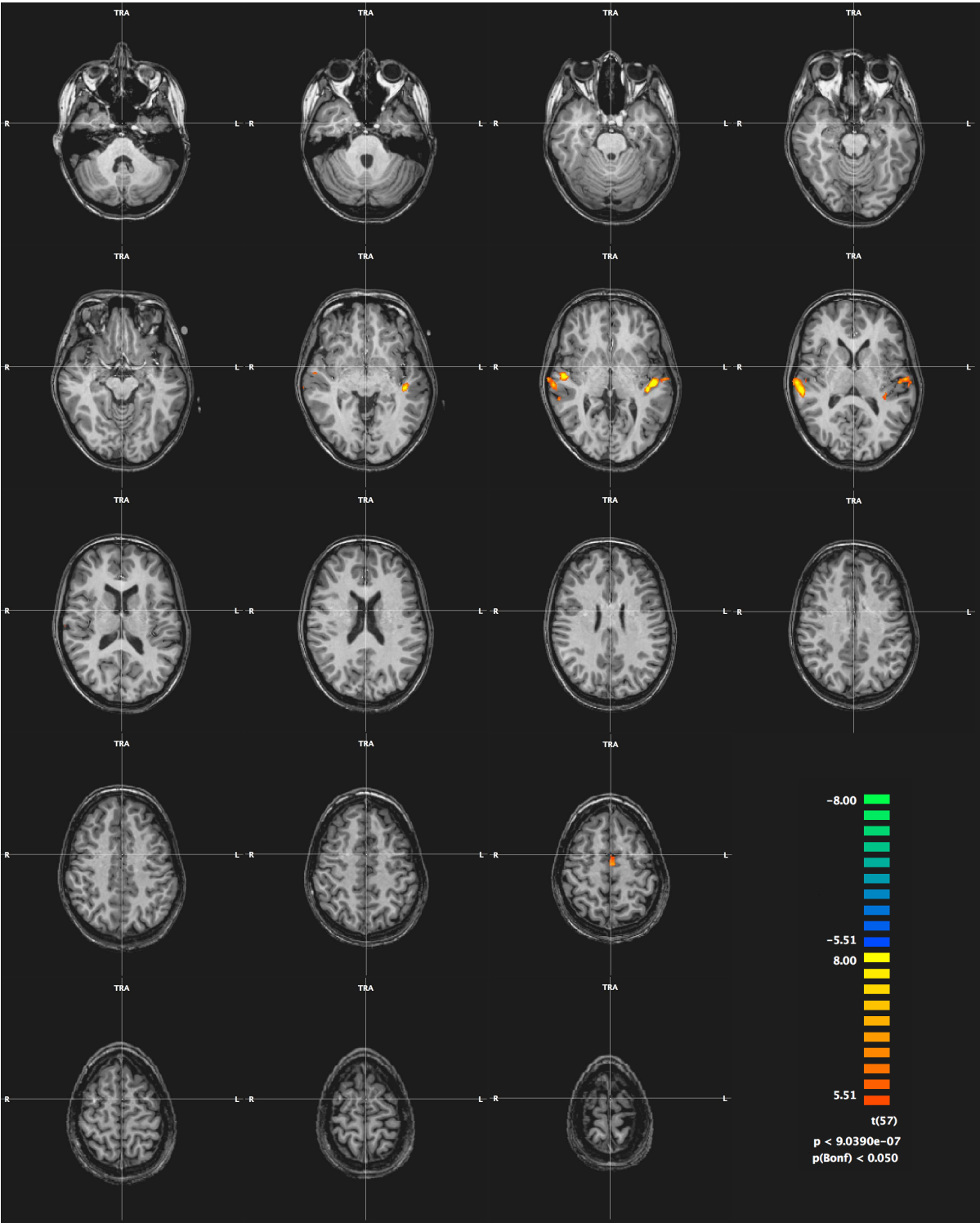
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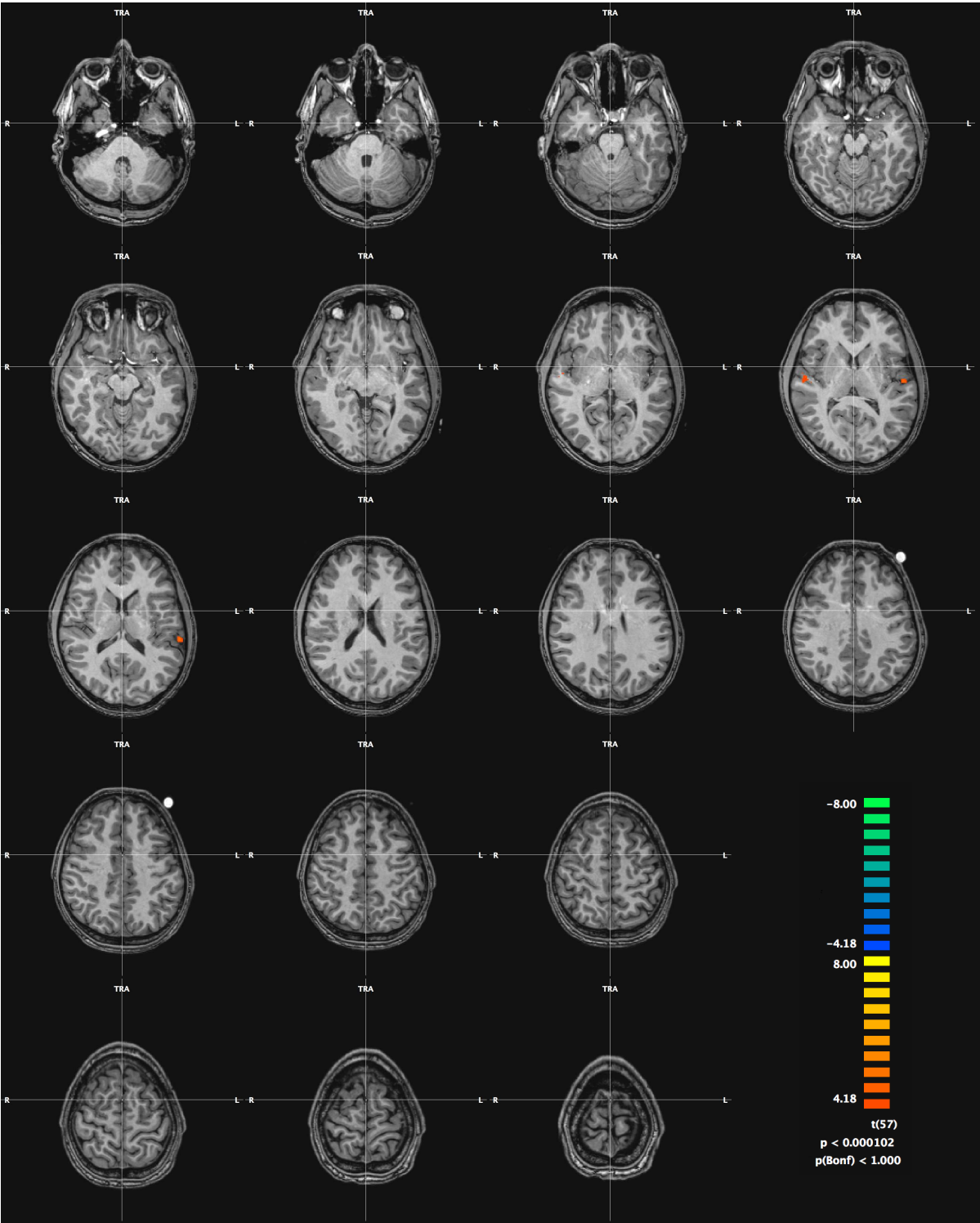
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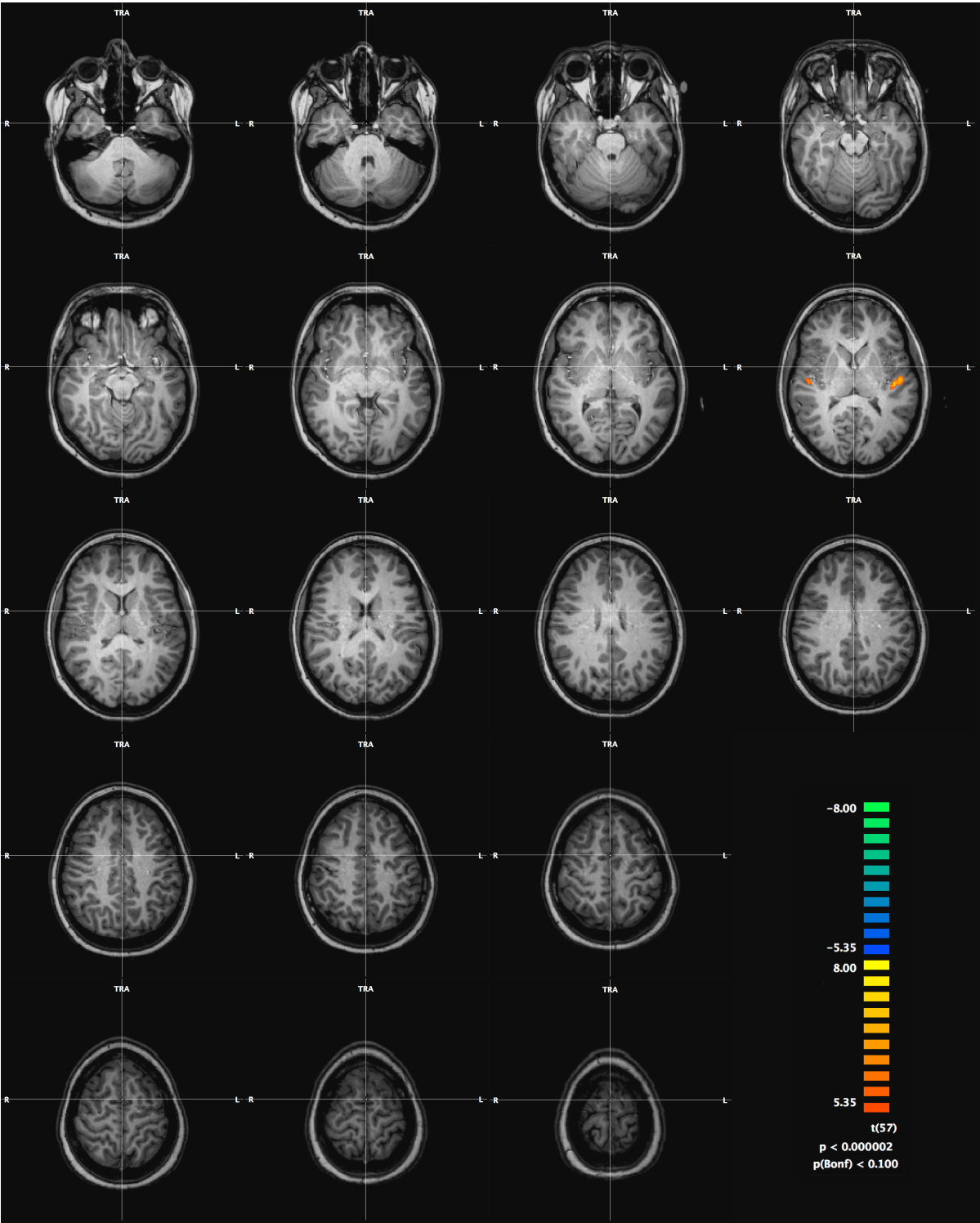
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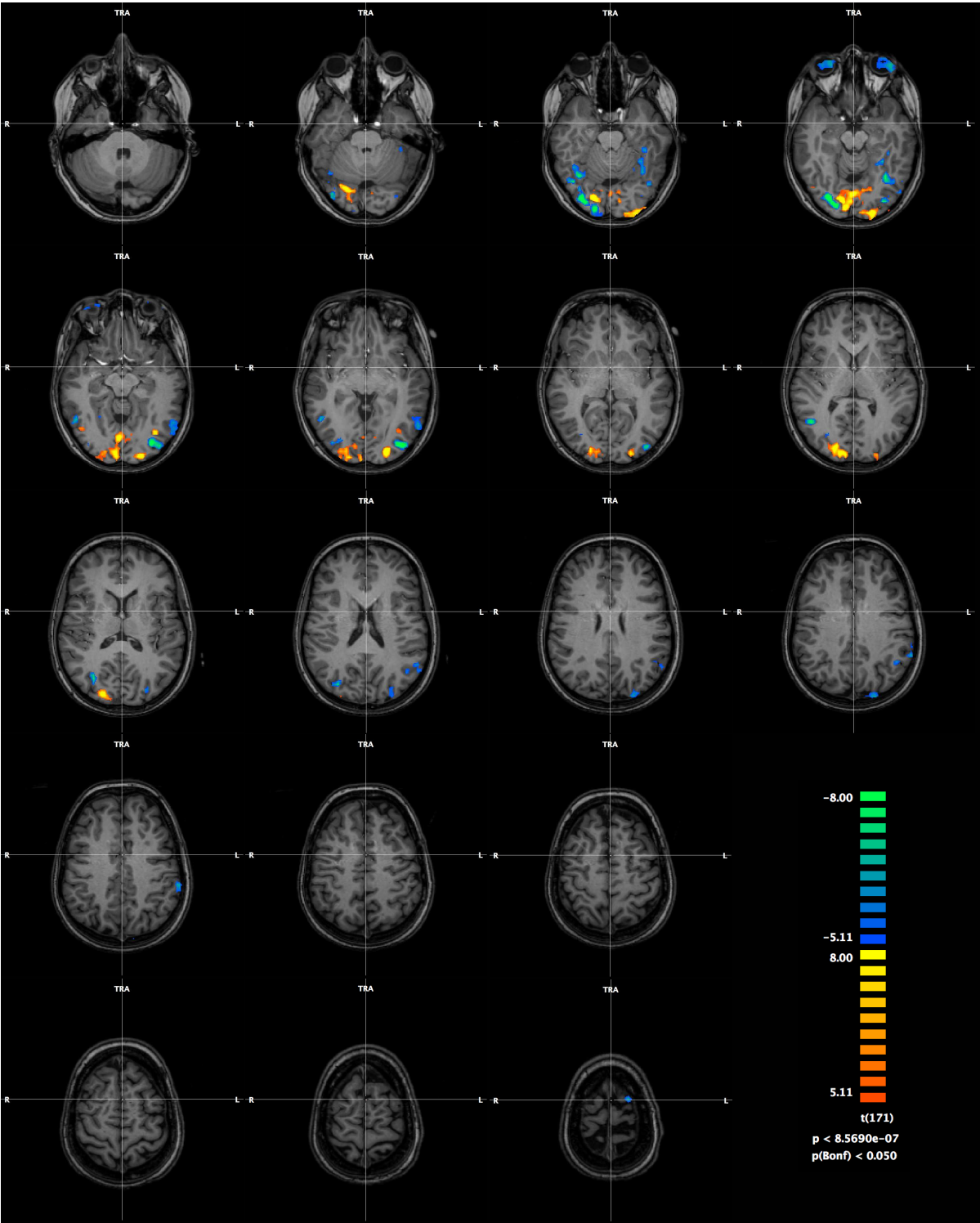
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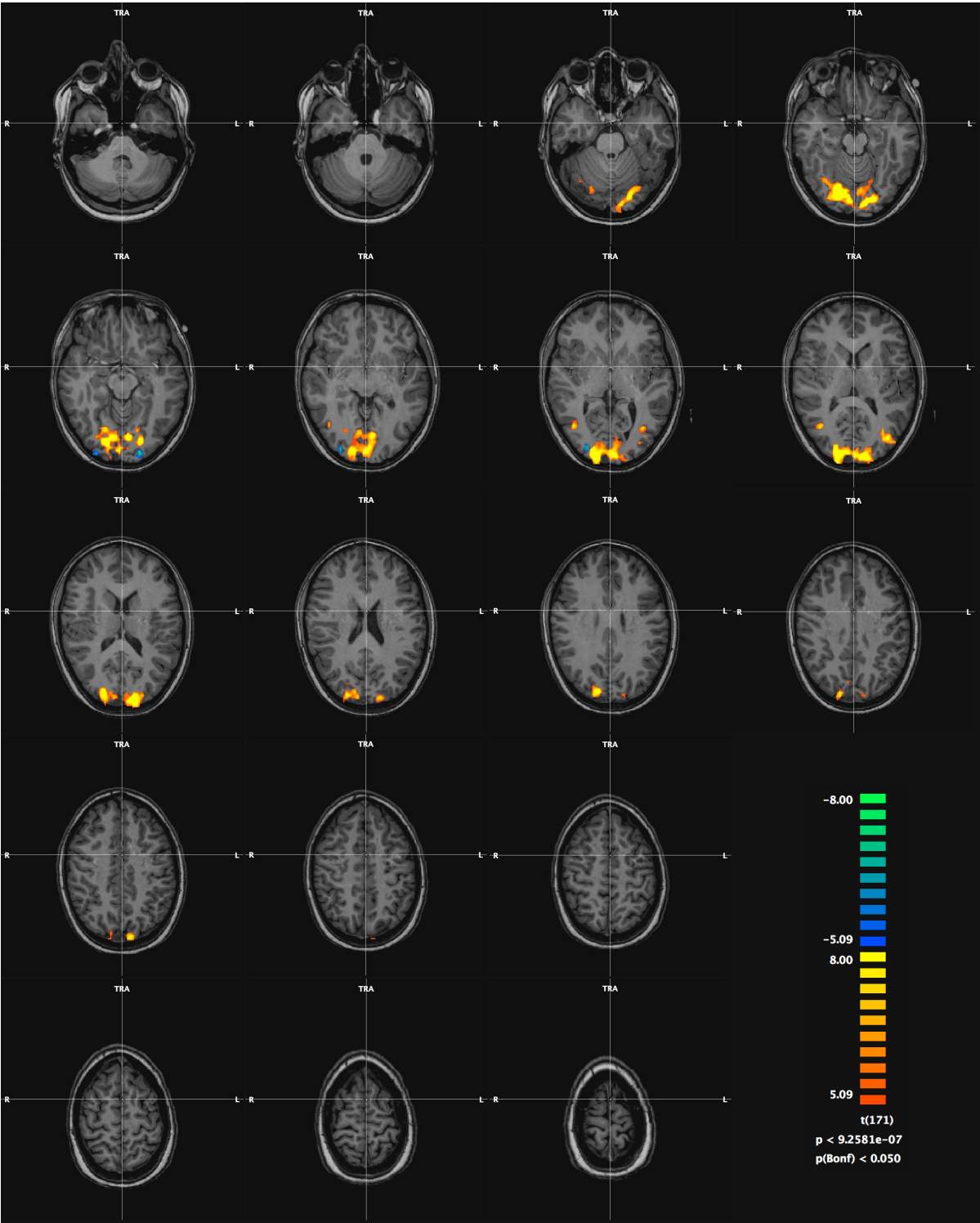
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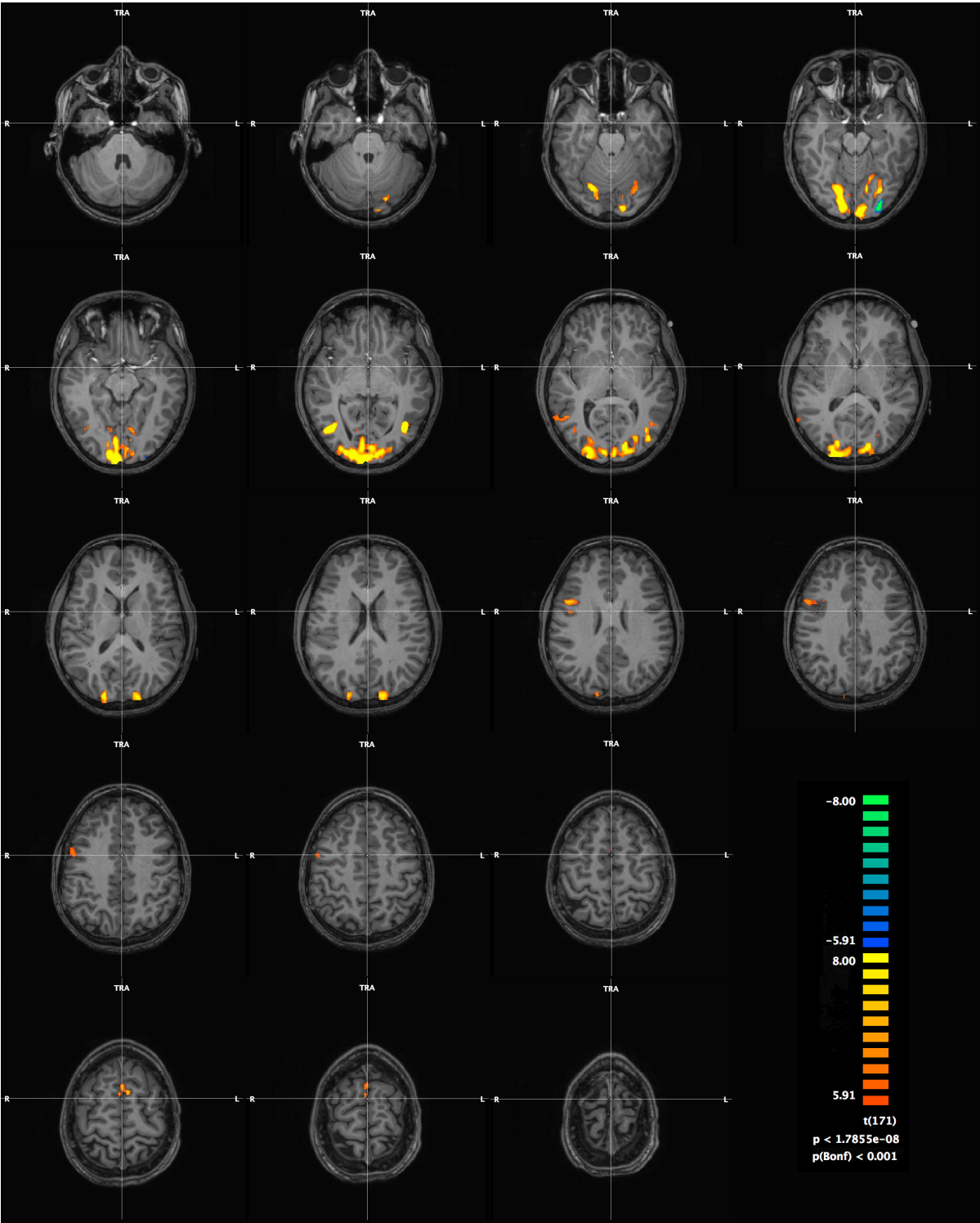
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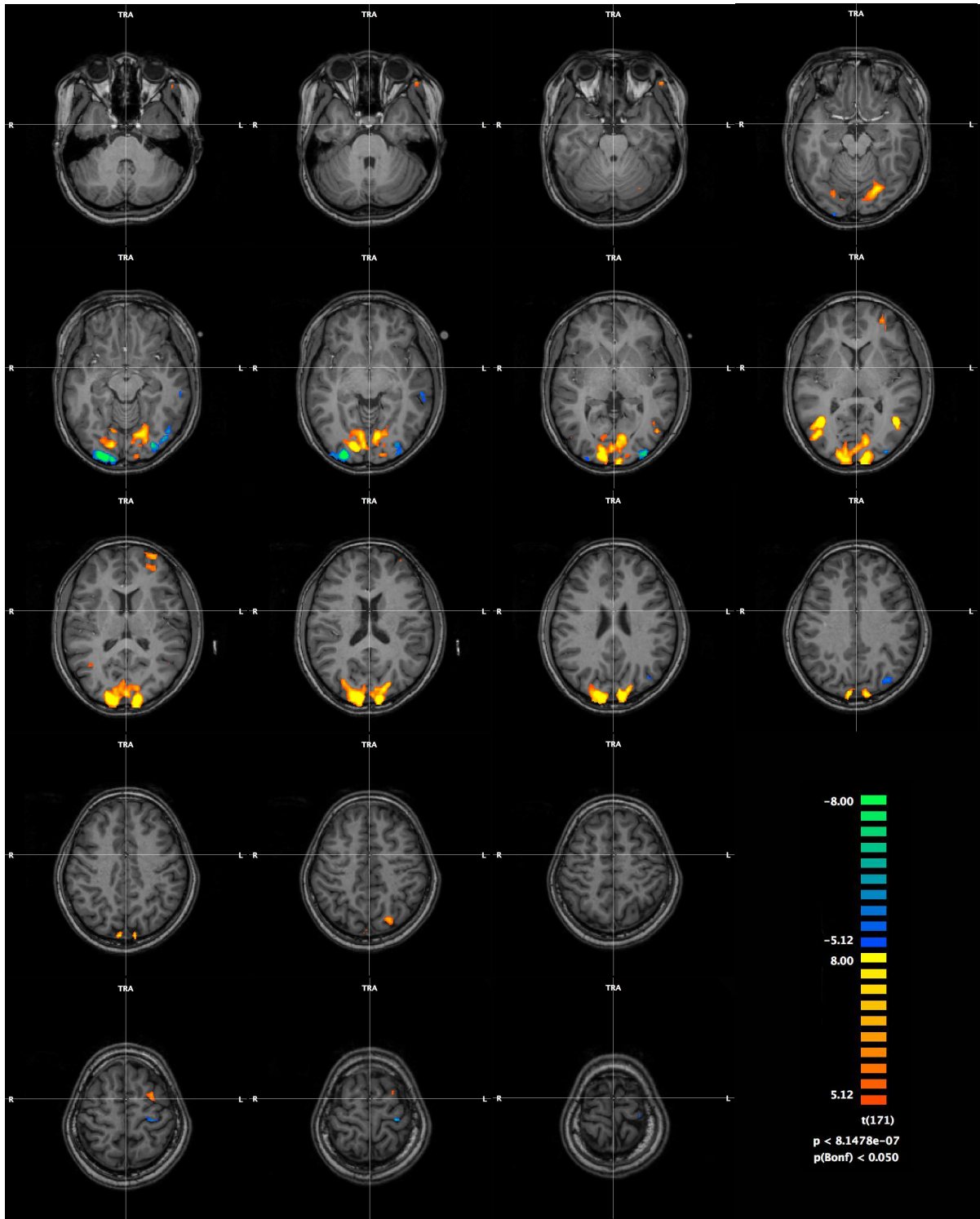
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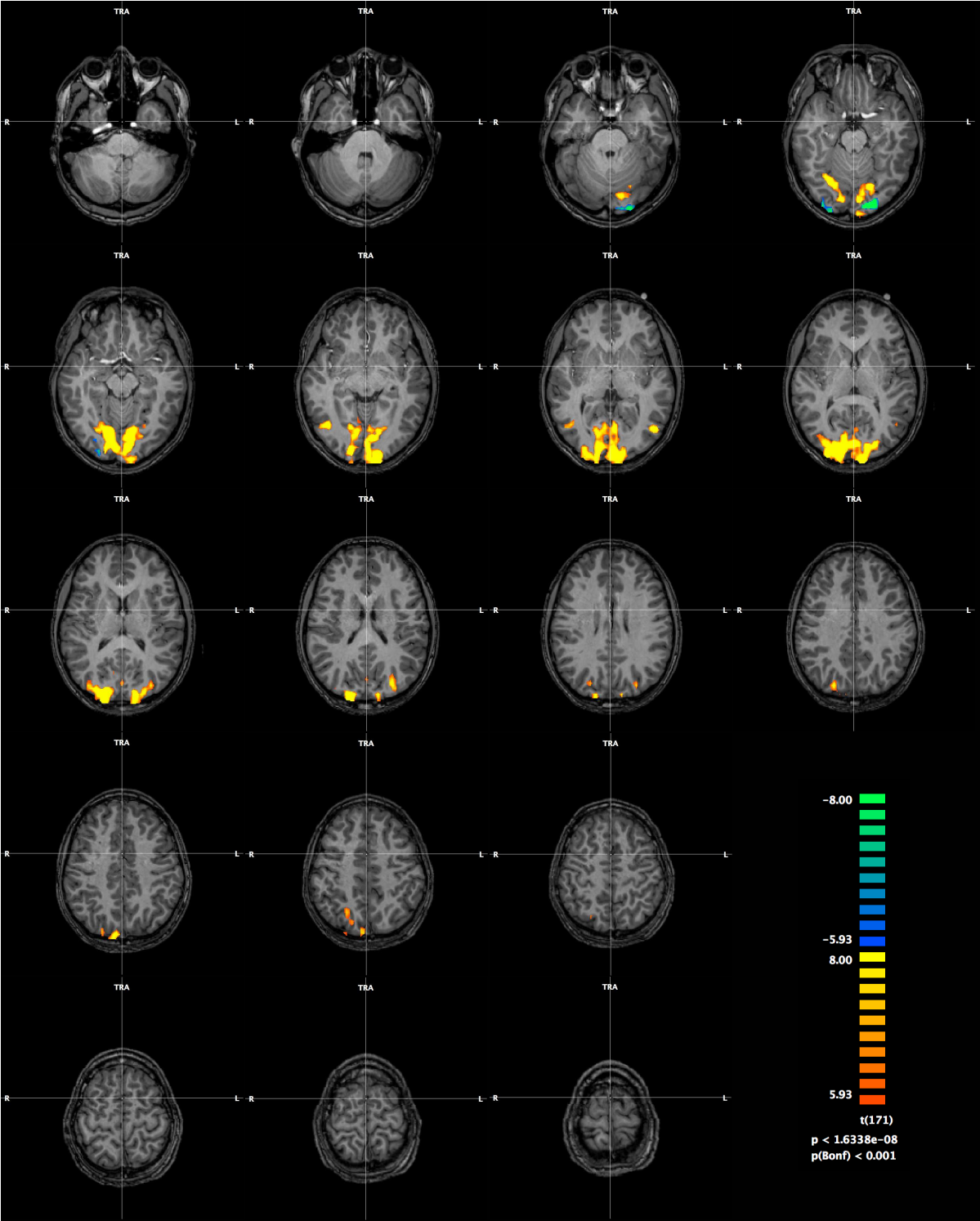
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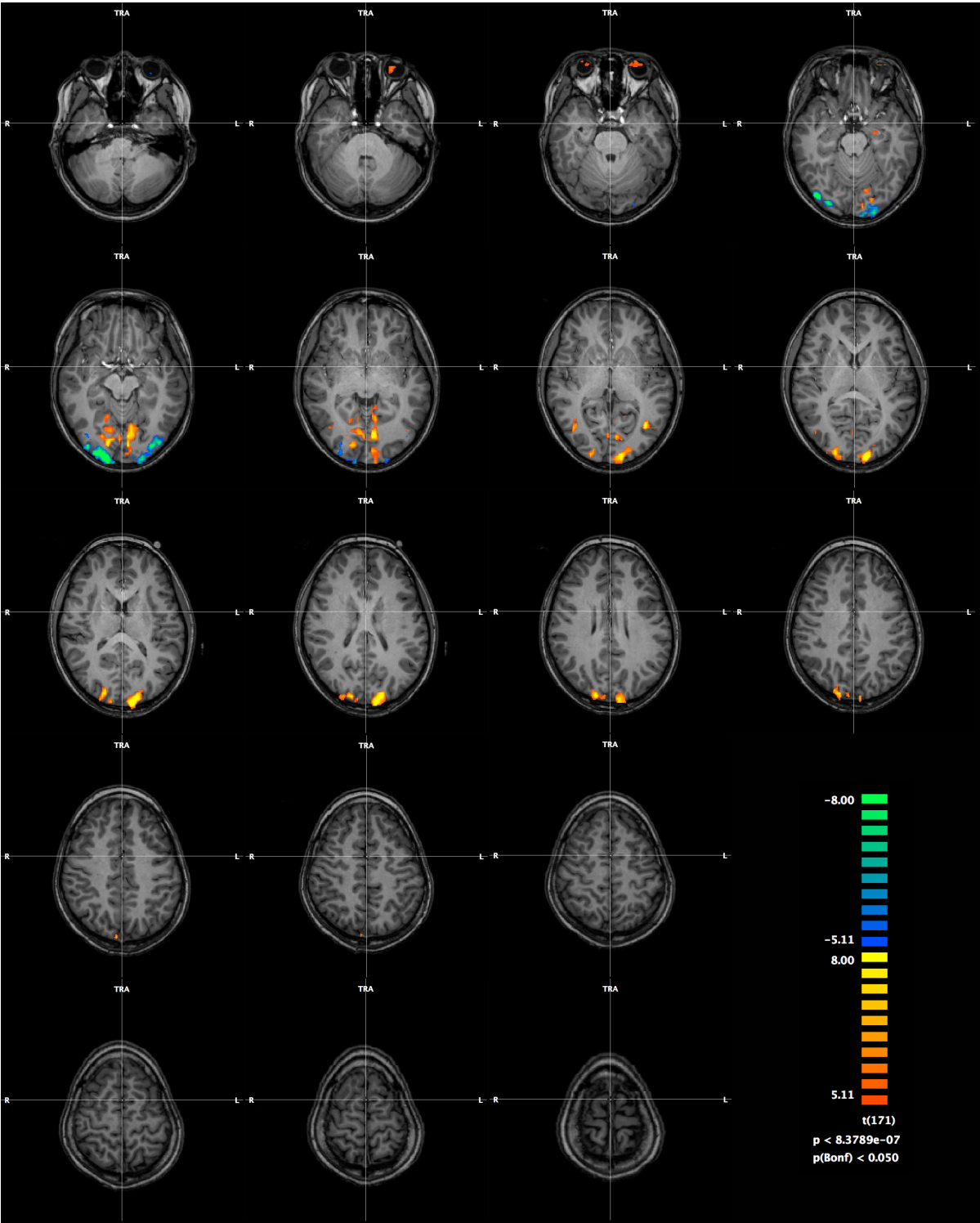
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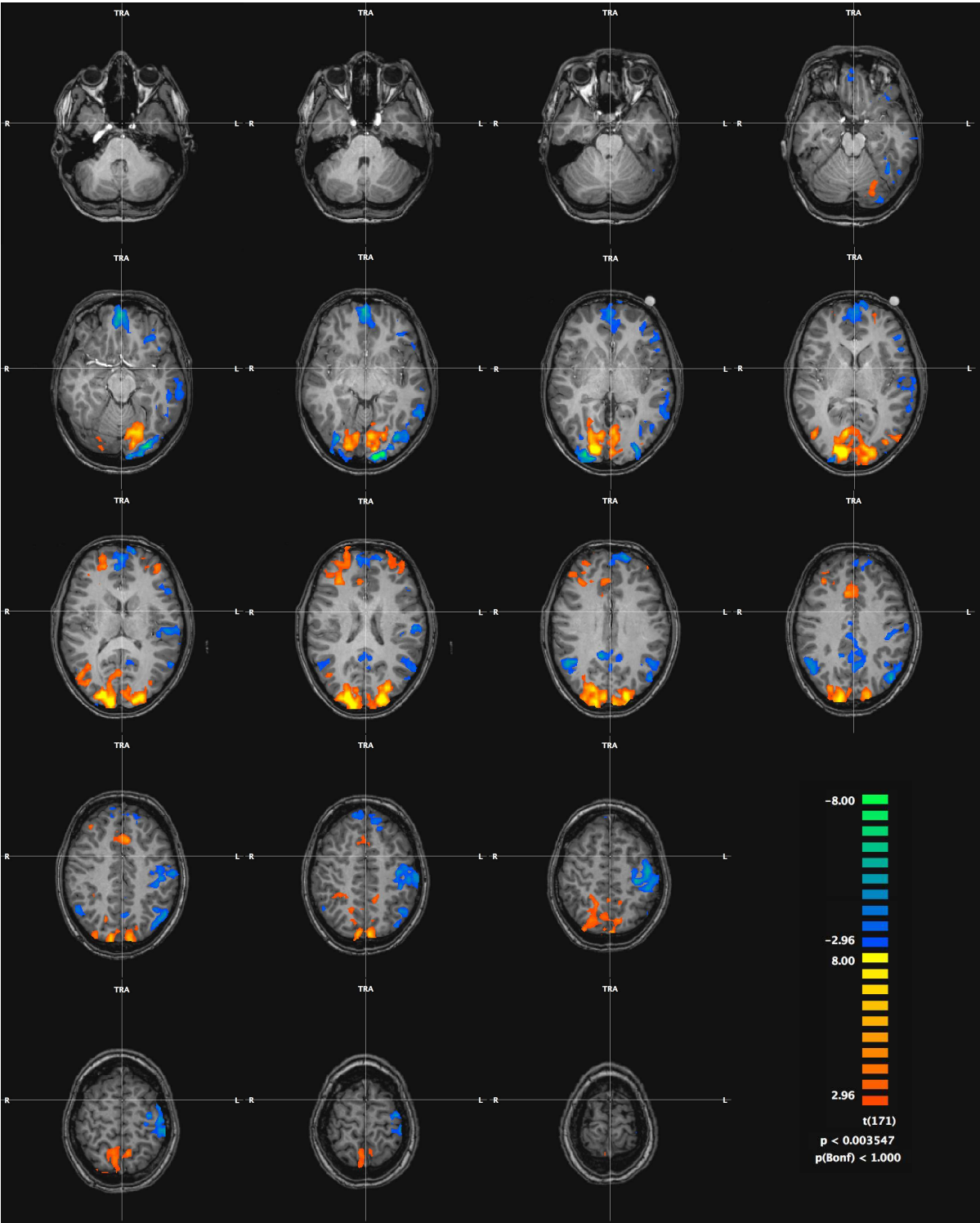
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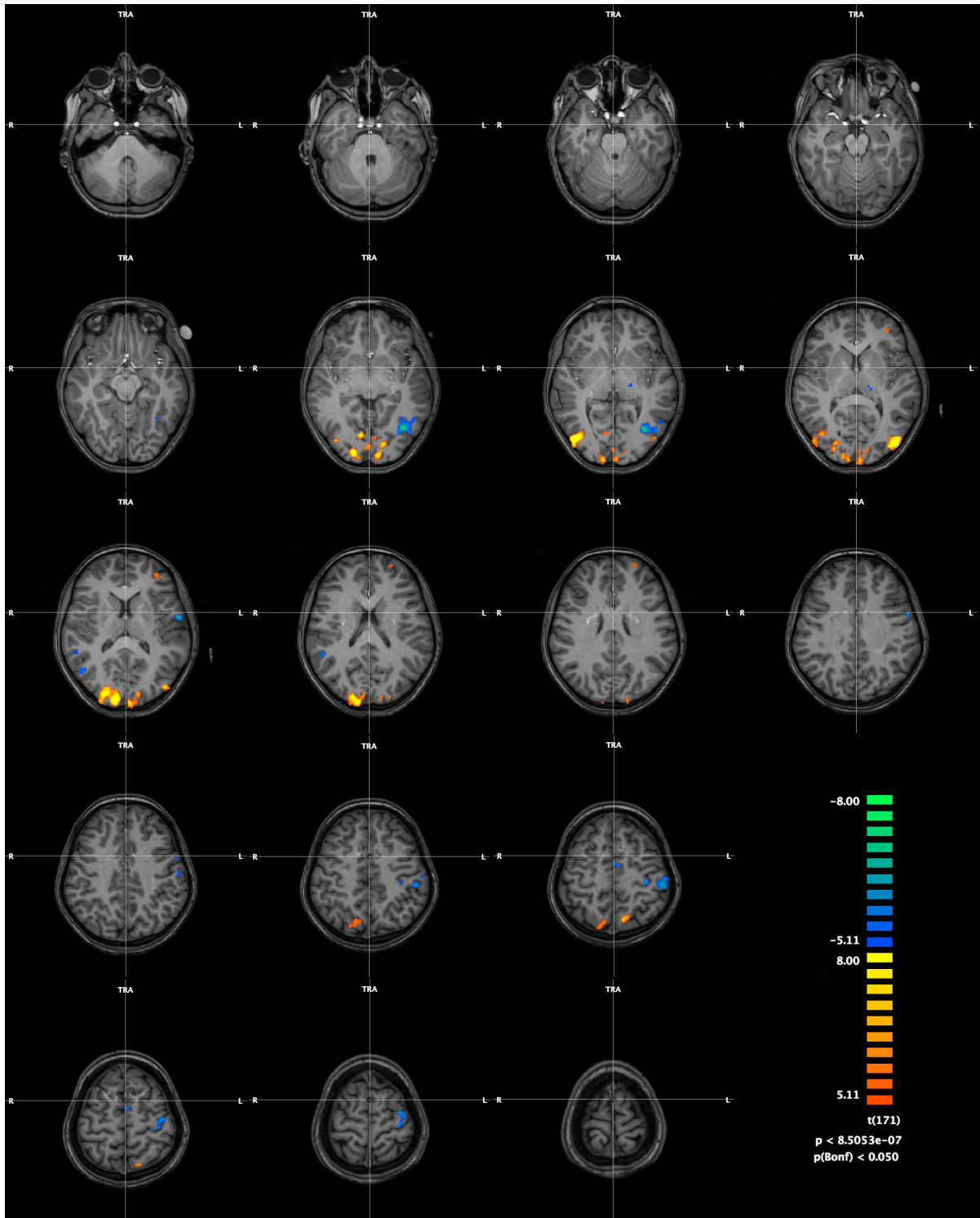
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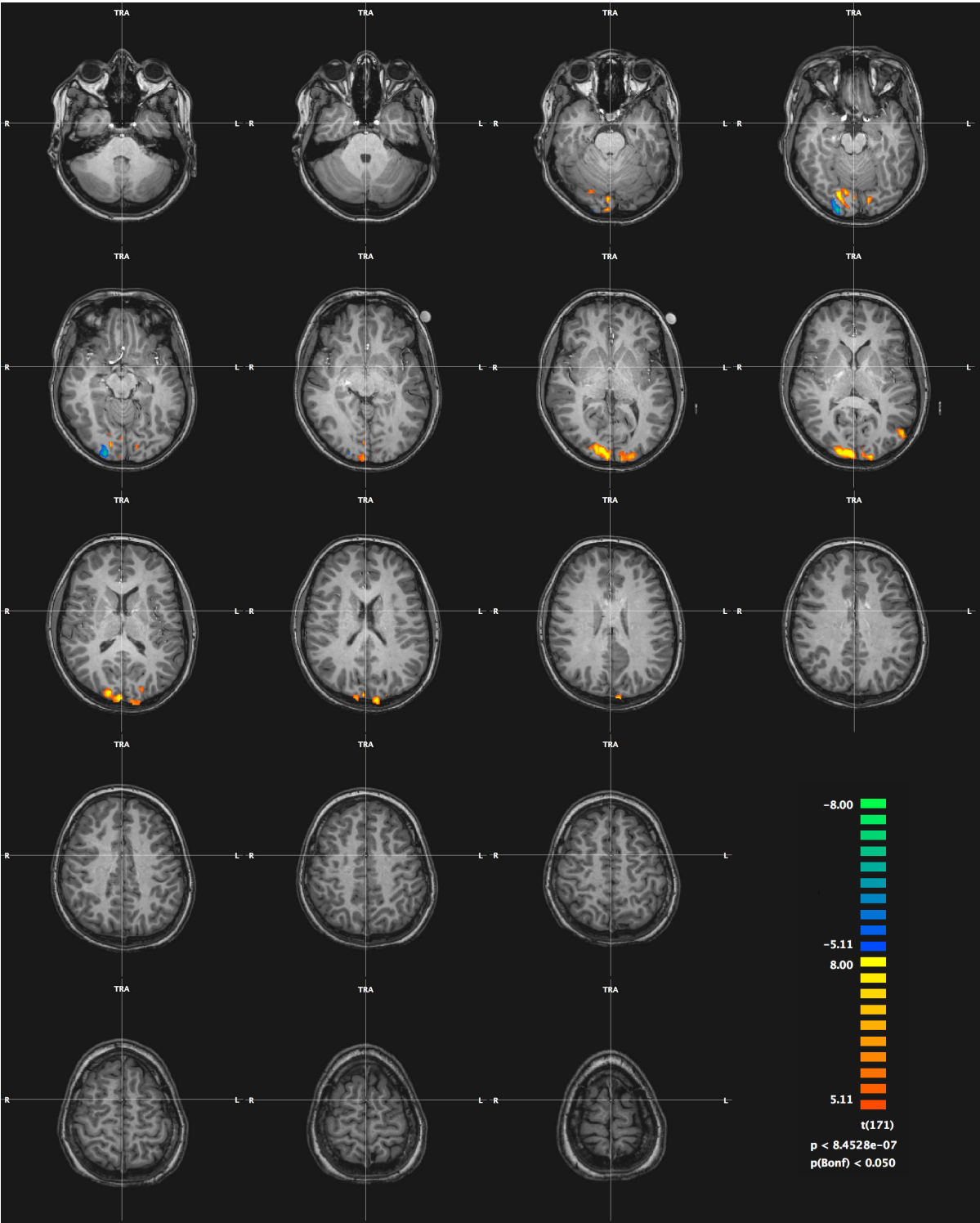
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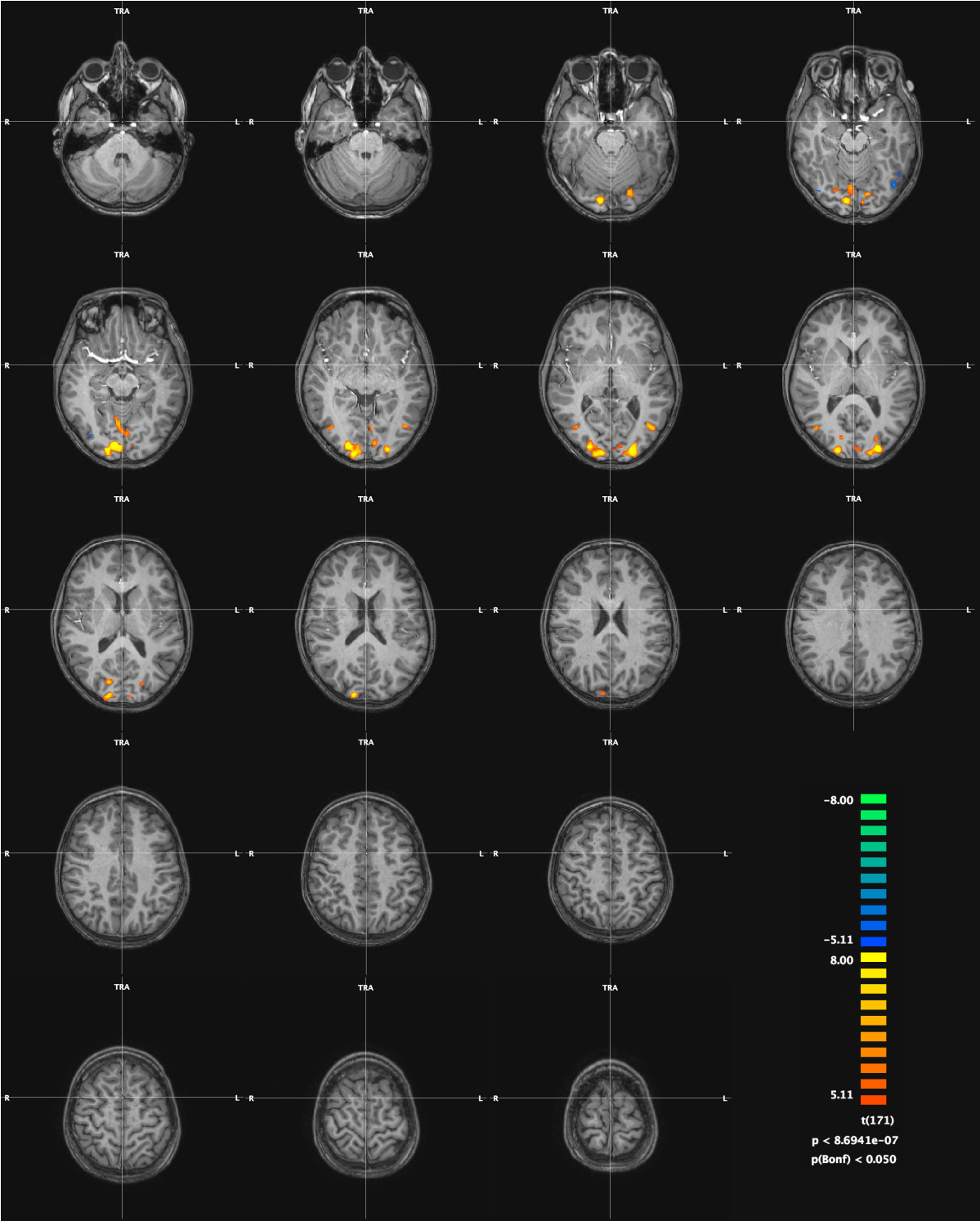
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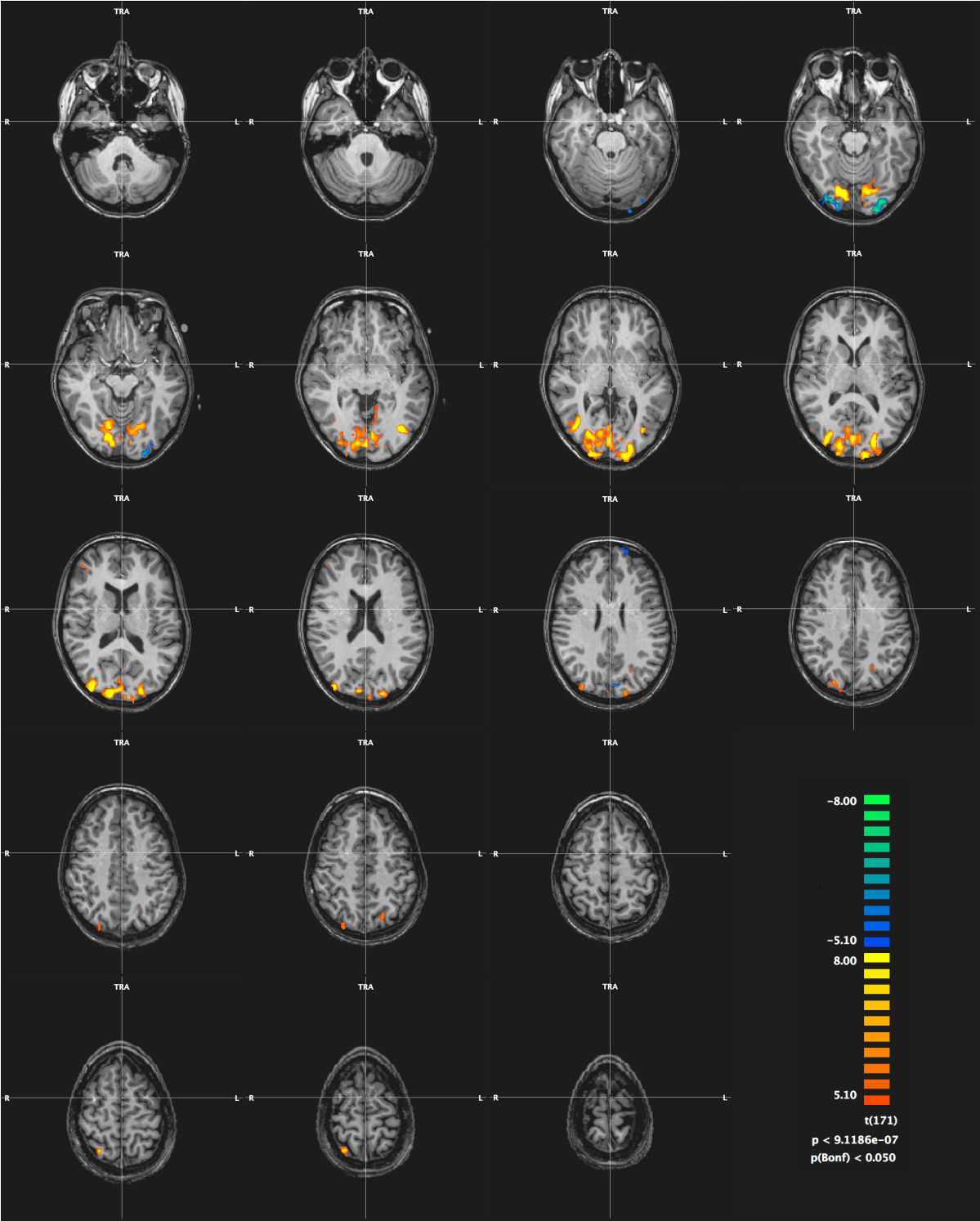
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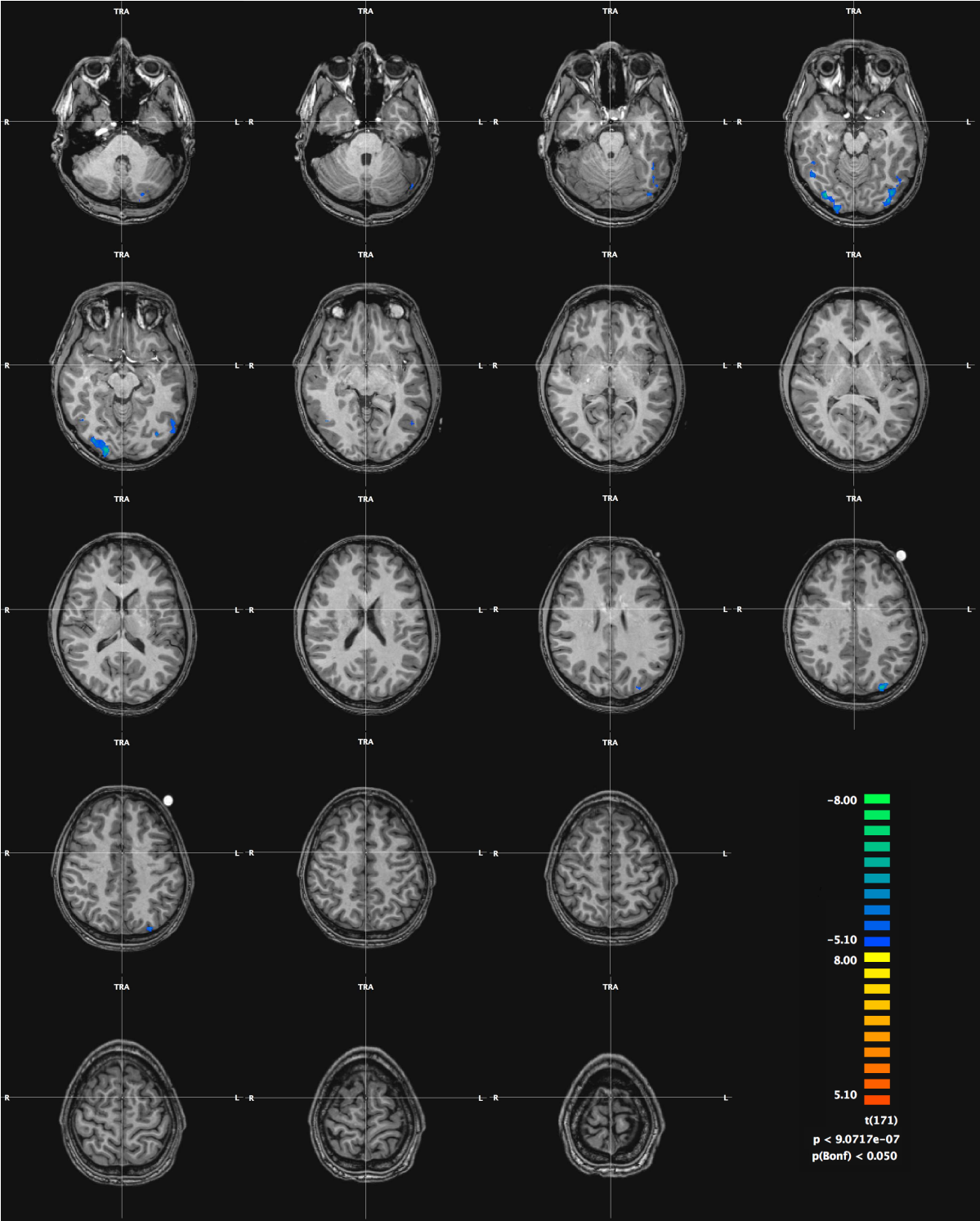
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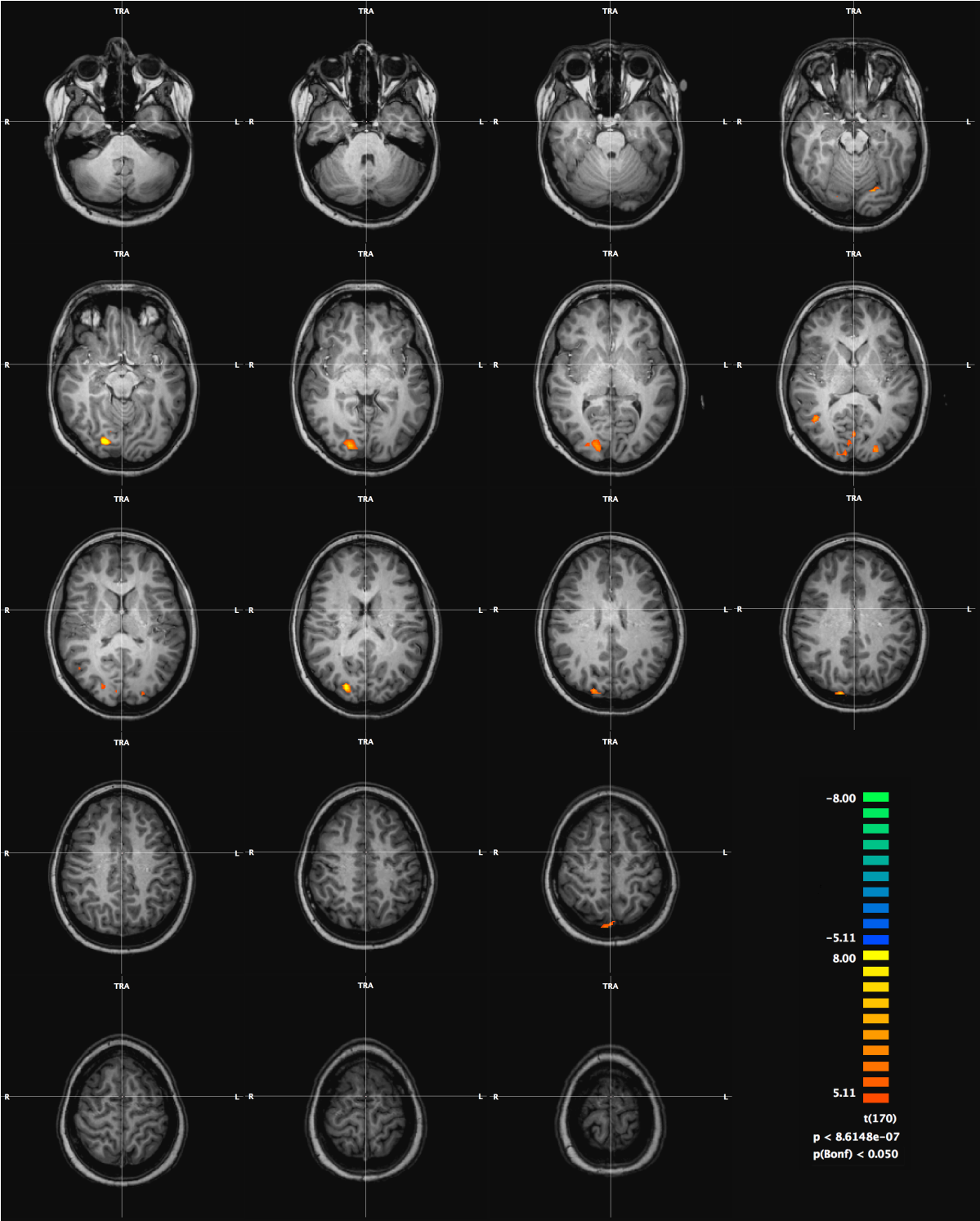
Phonological reading (C02)
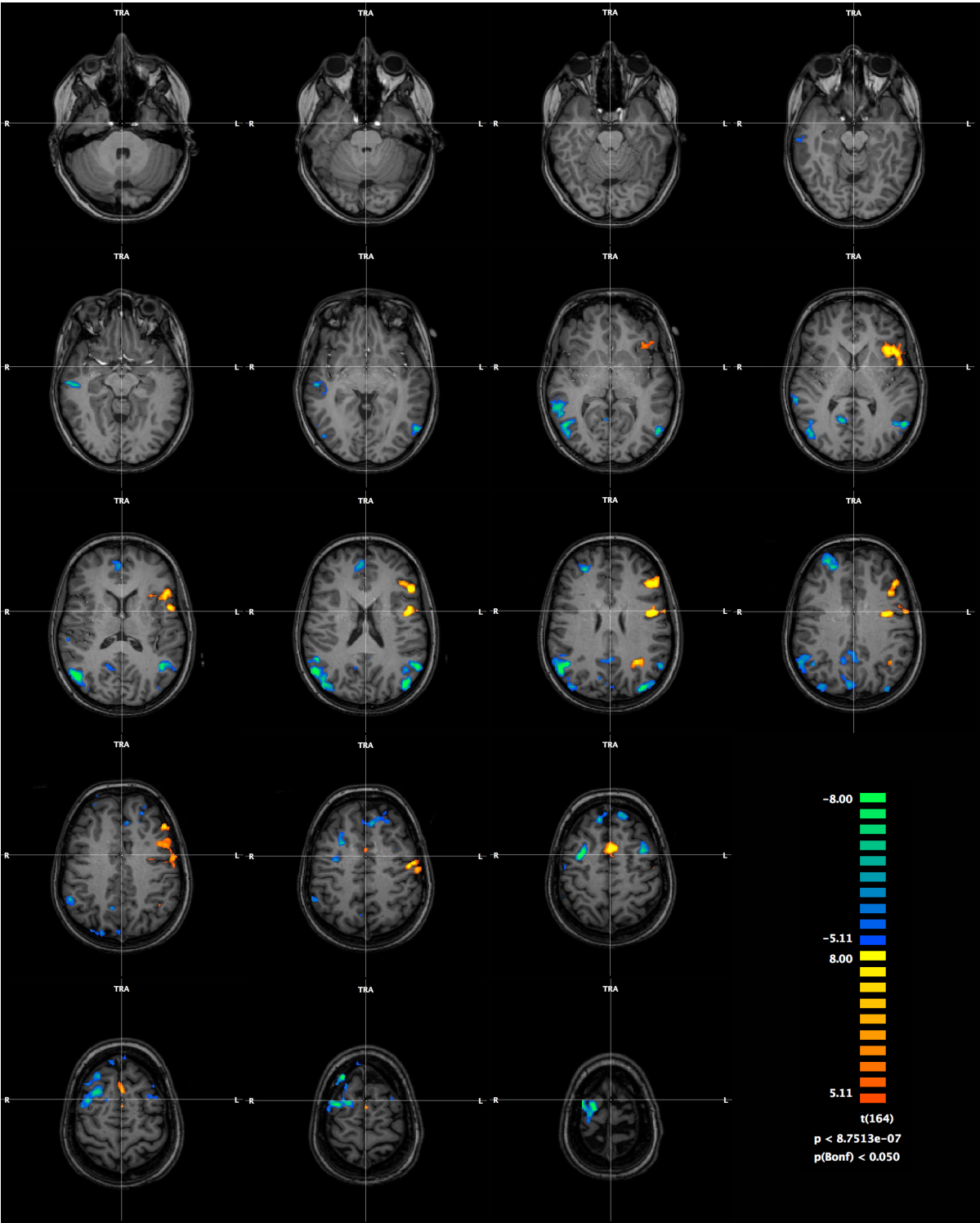
Phonological reading (C04)
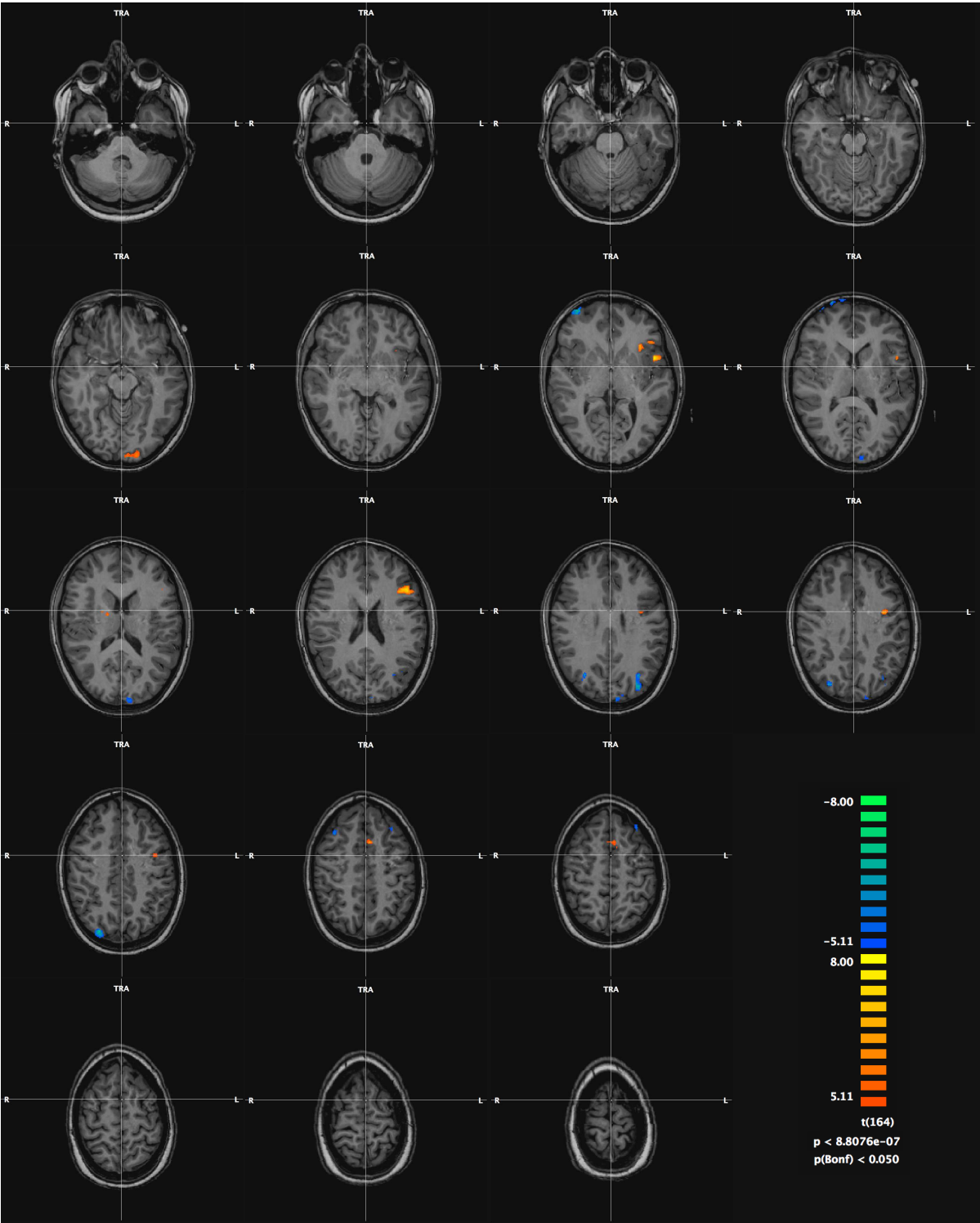
Phonological reading (C05)
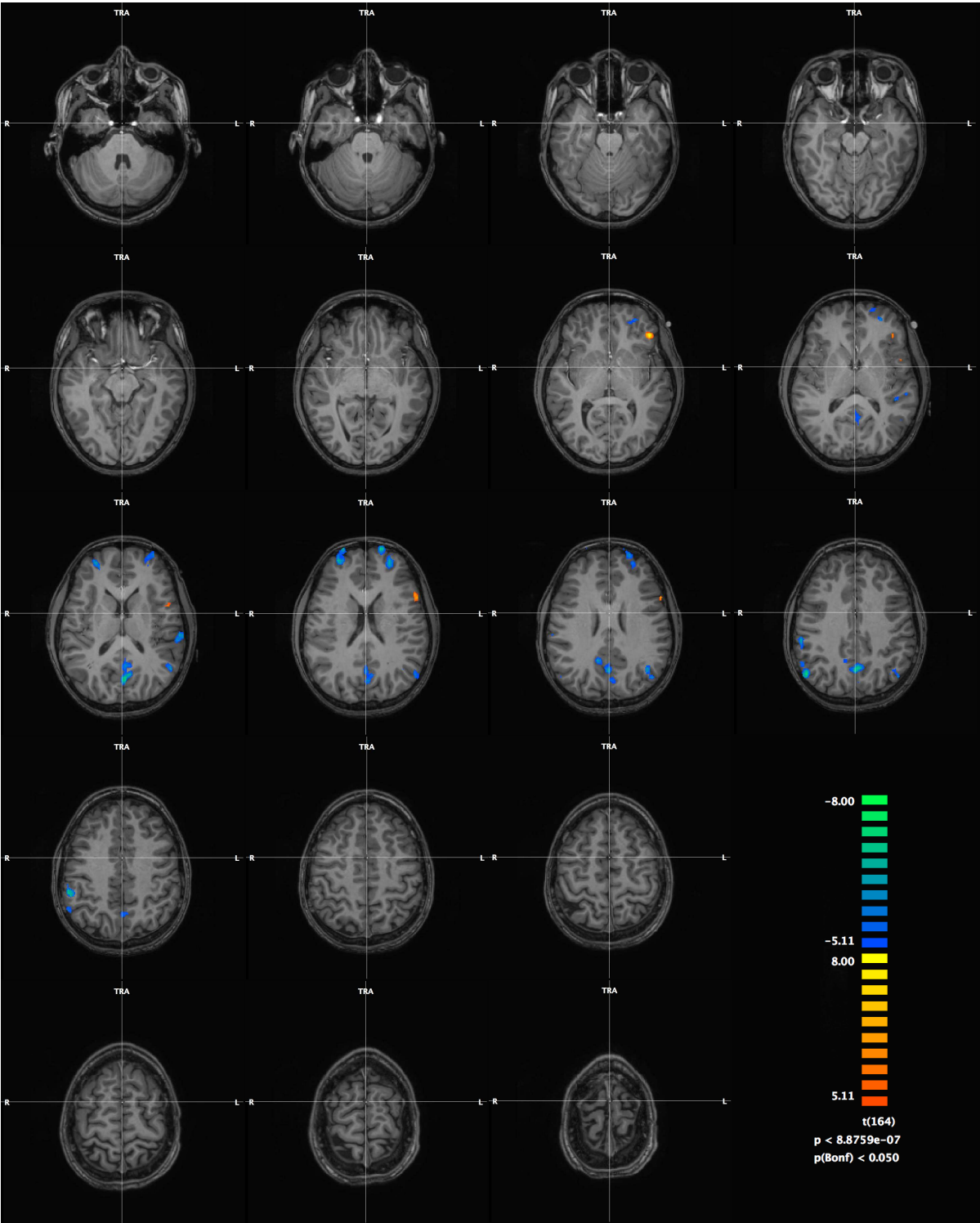
Phonological reading (C06)
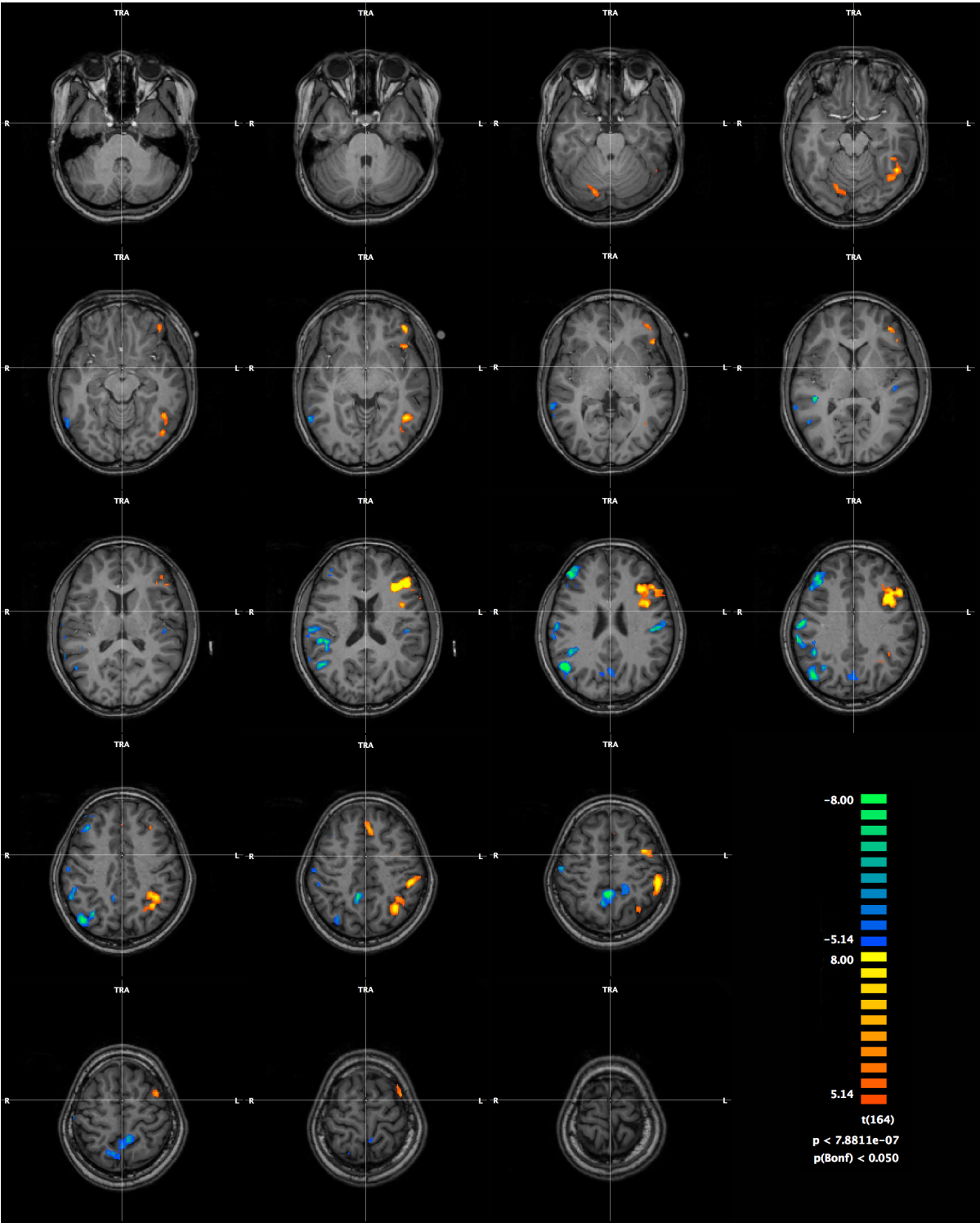
Phonological reading (C09)
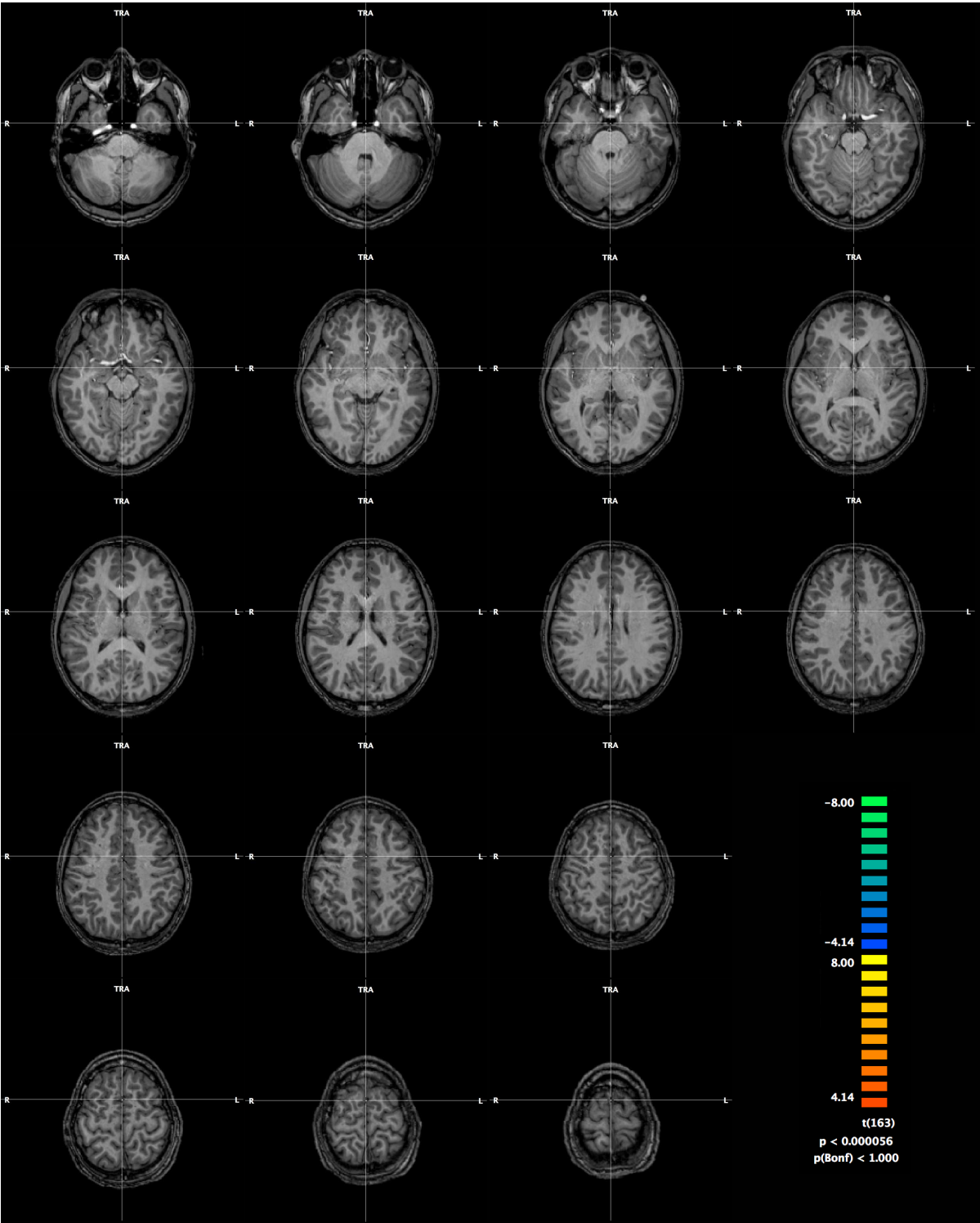
Phonological reading (C10)
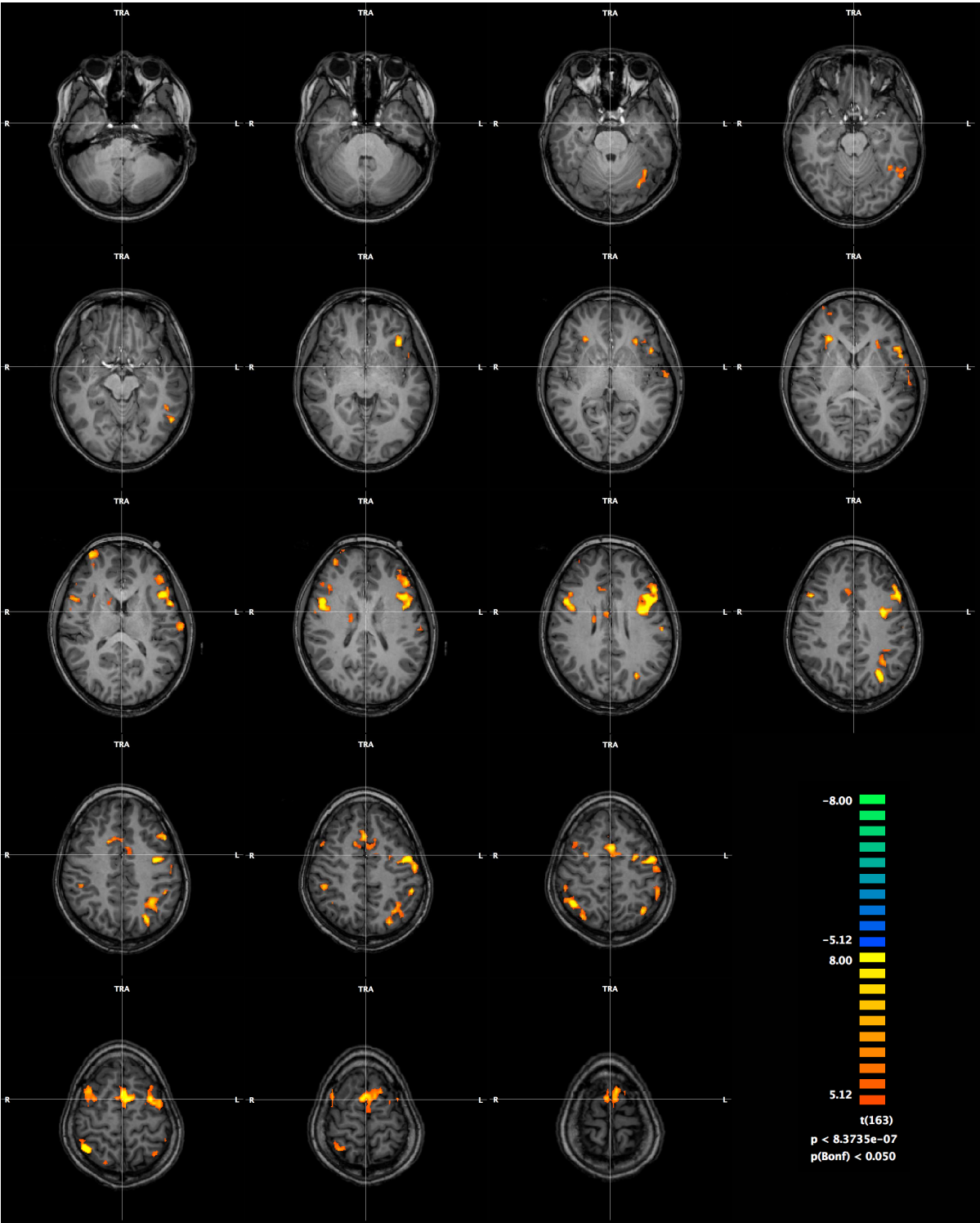
Phonological reading (C12)
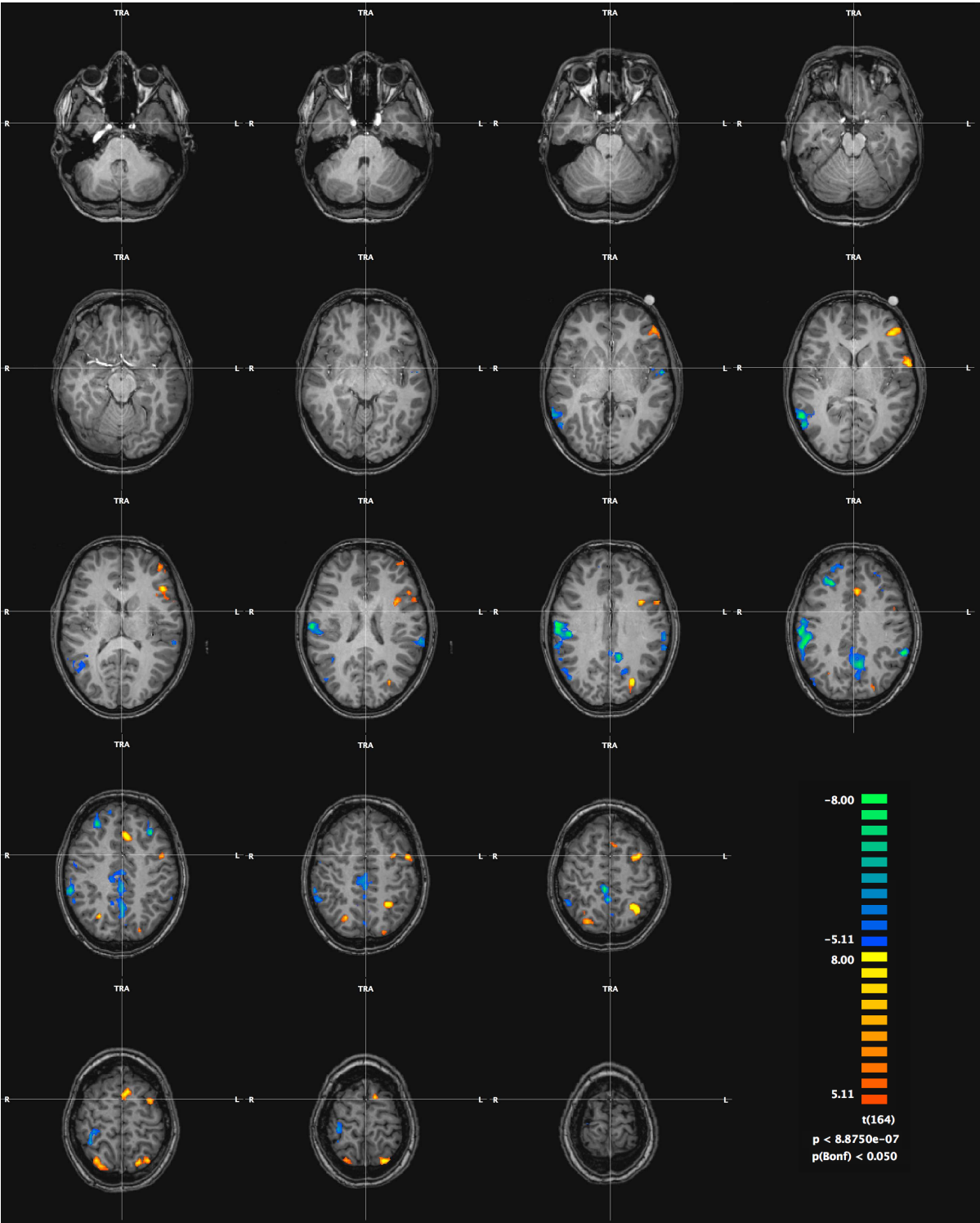
Phonological reading (C14)
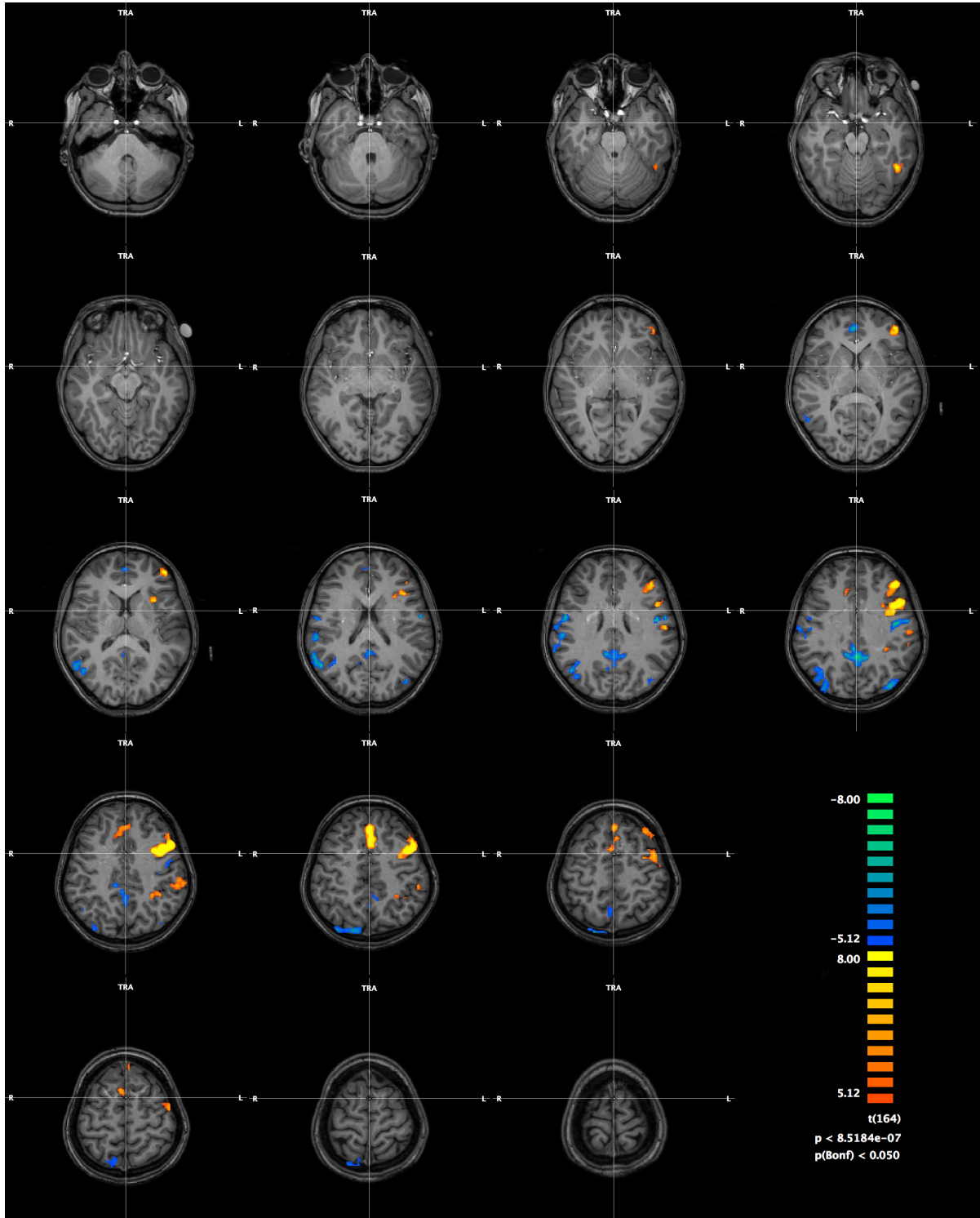
Phonological reading (C15)
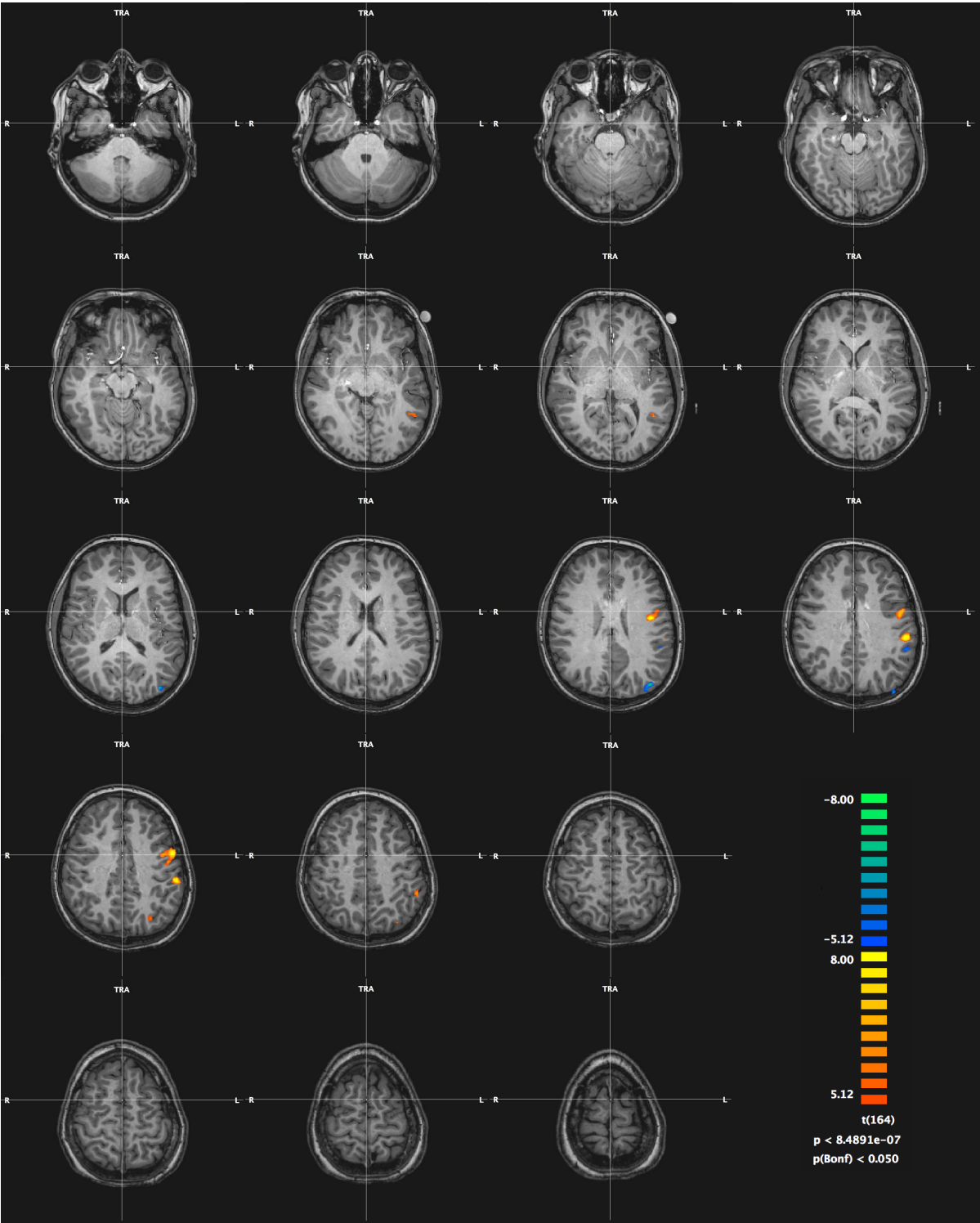
Phonological reading (E01)
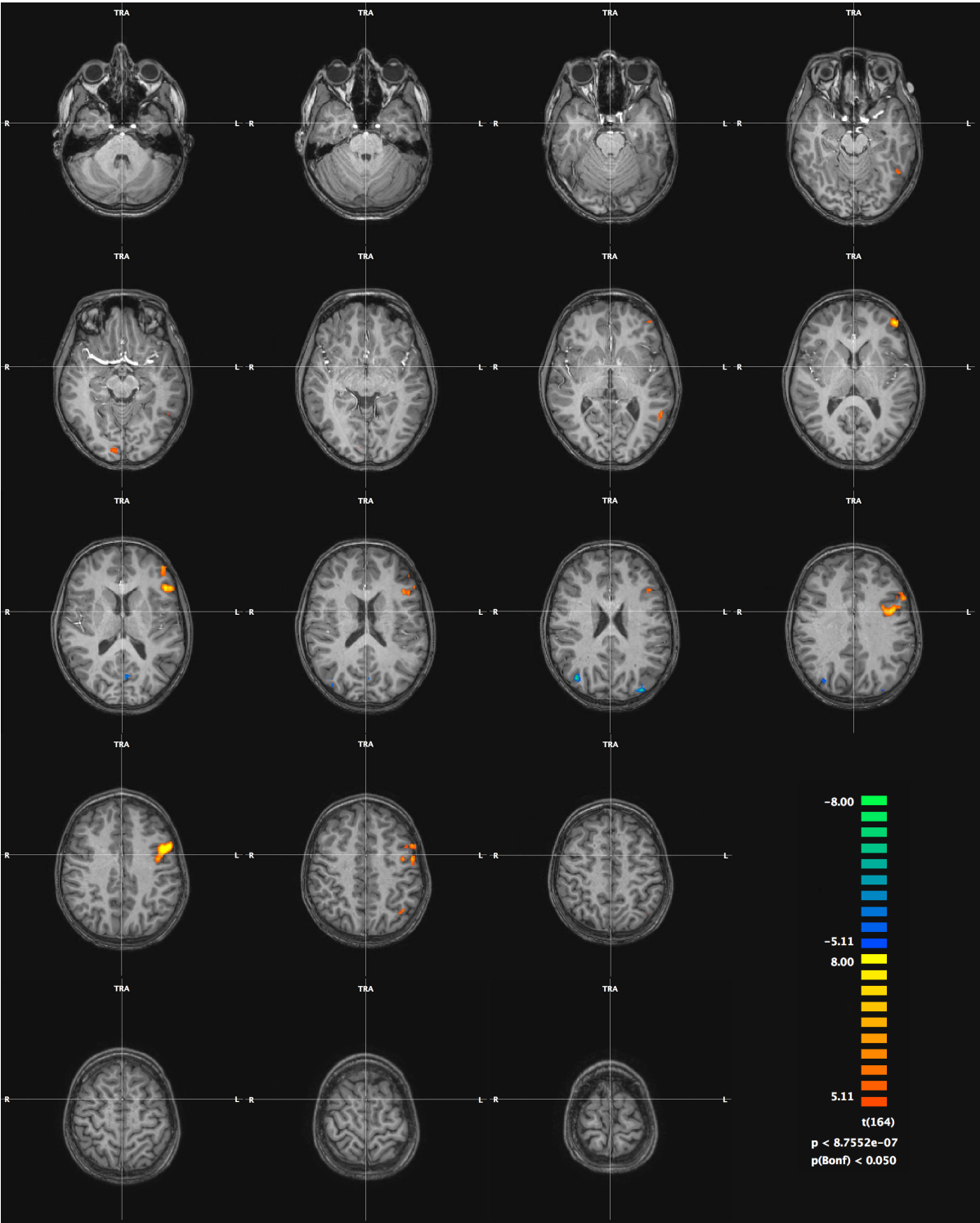
Phonological reading (E02)
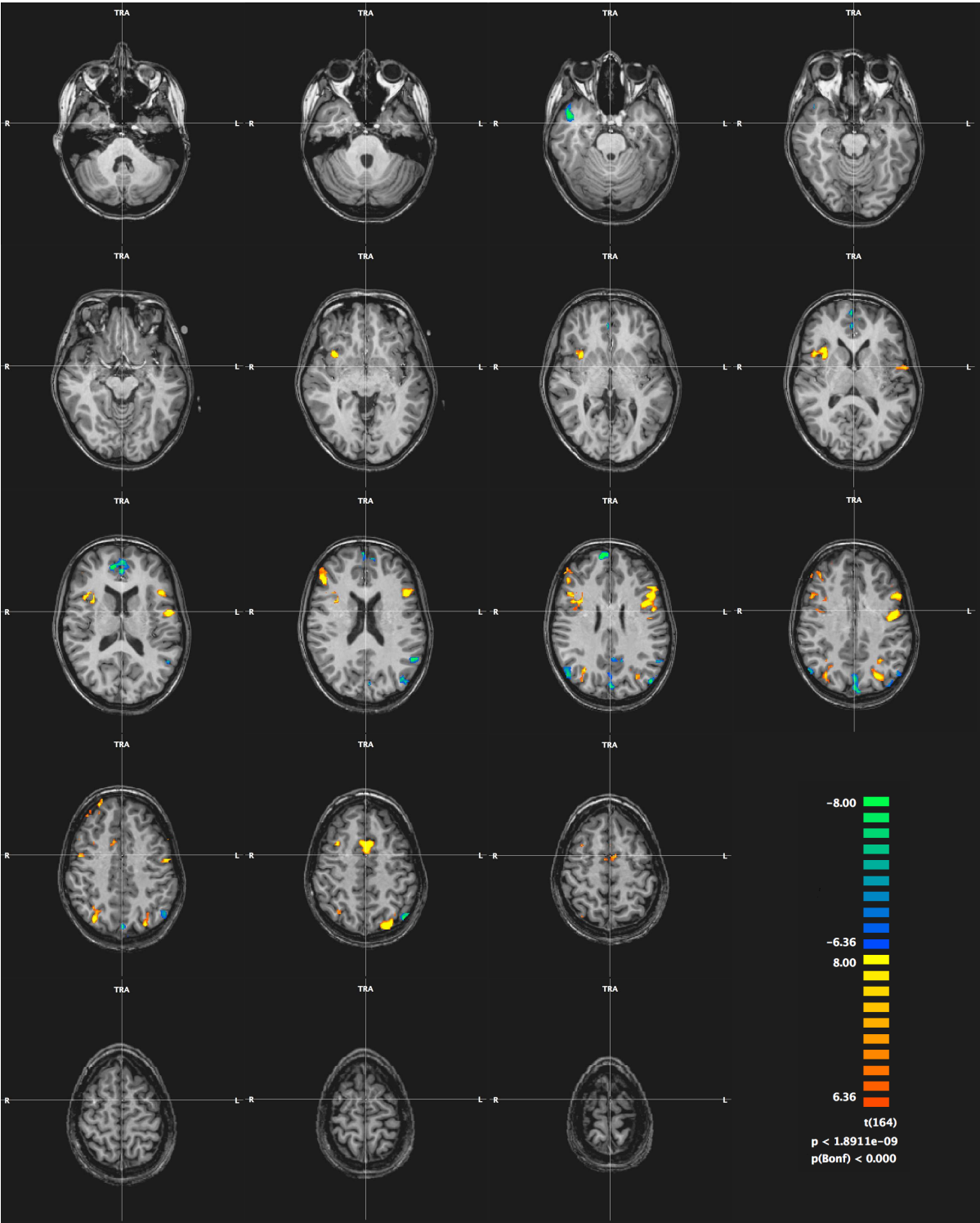
Phonological reading (E05)
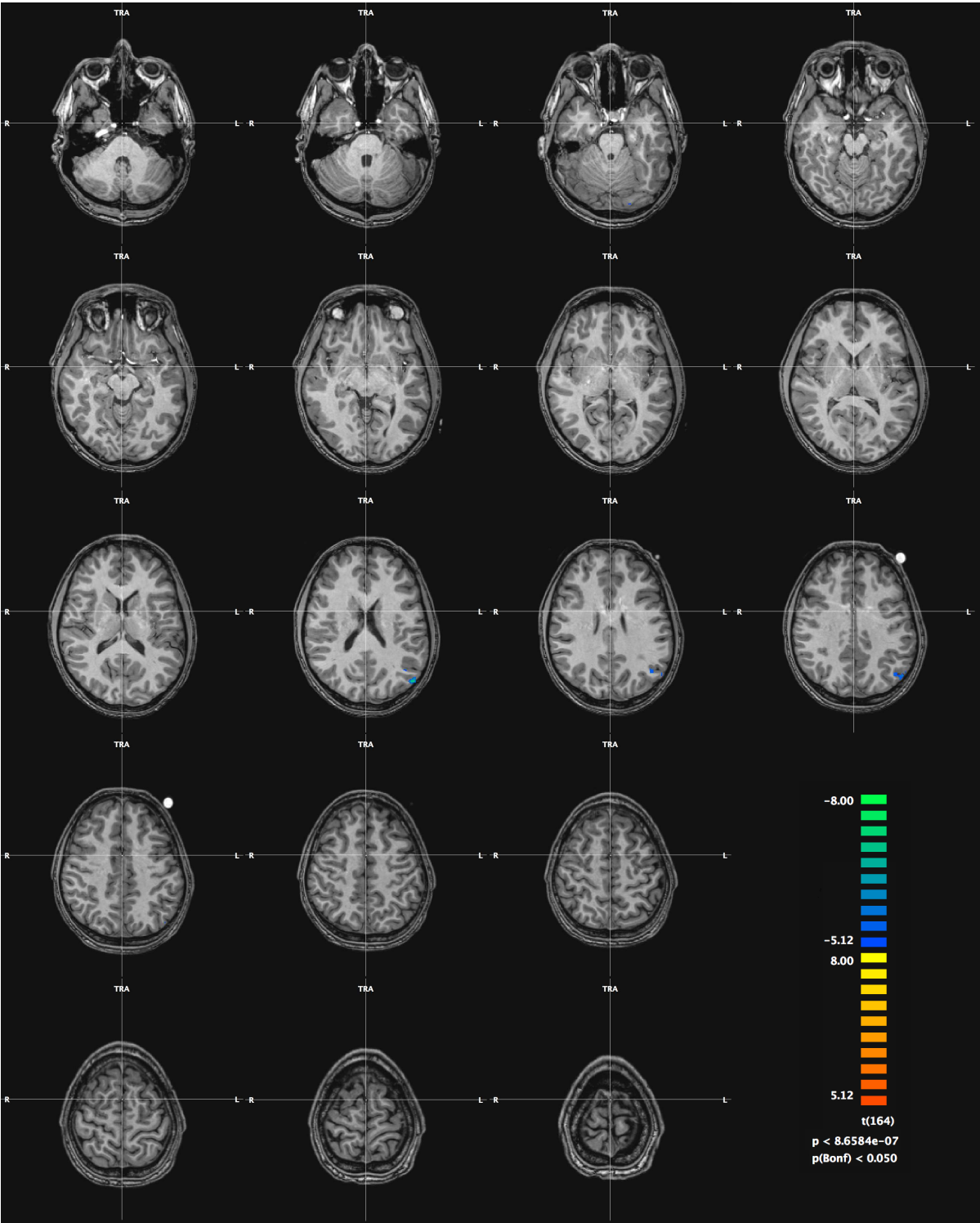
Phonological reading (E17)
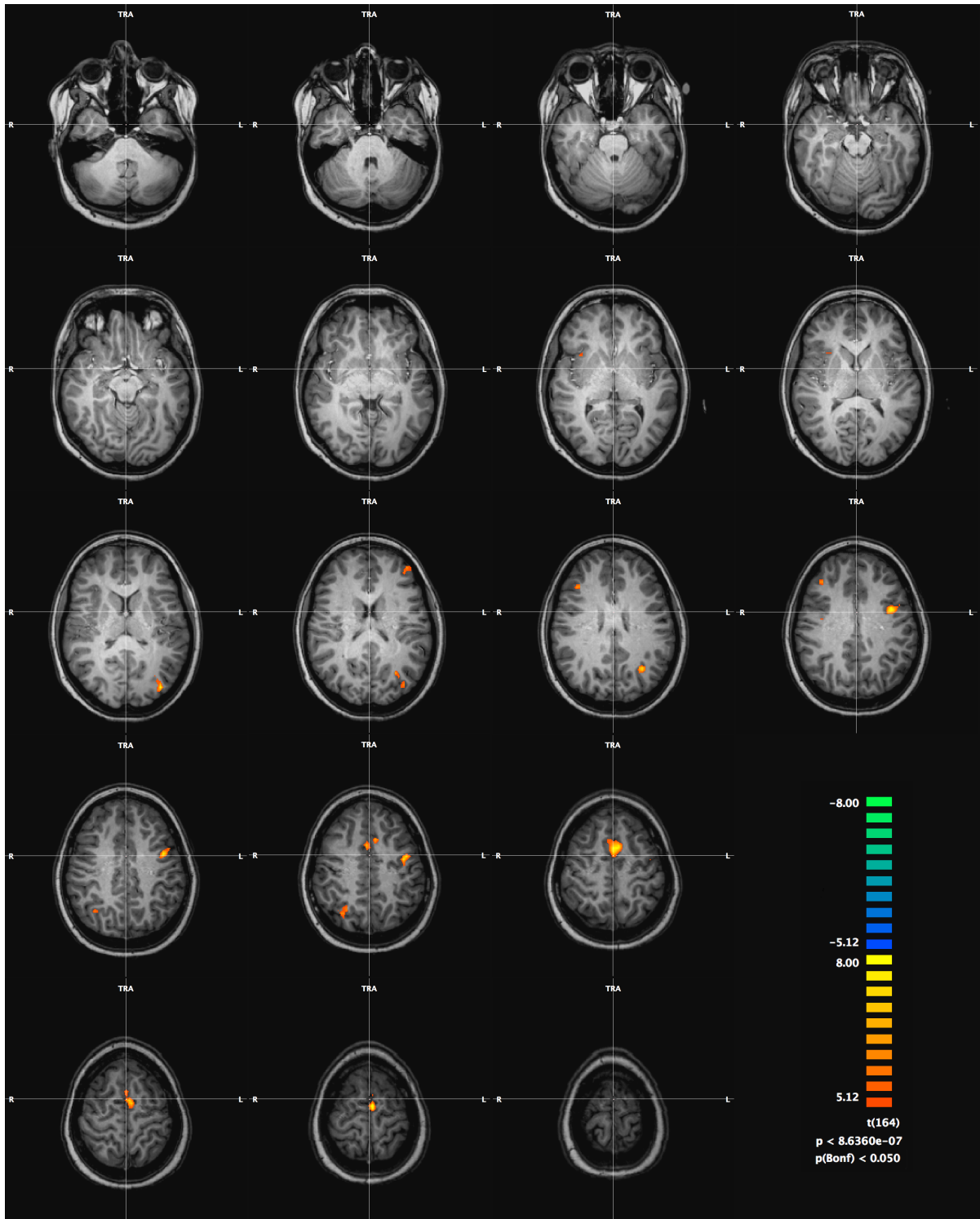
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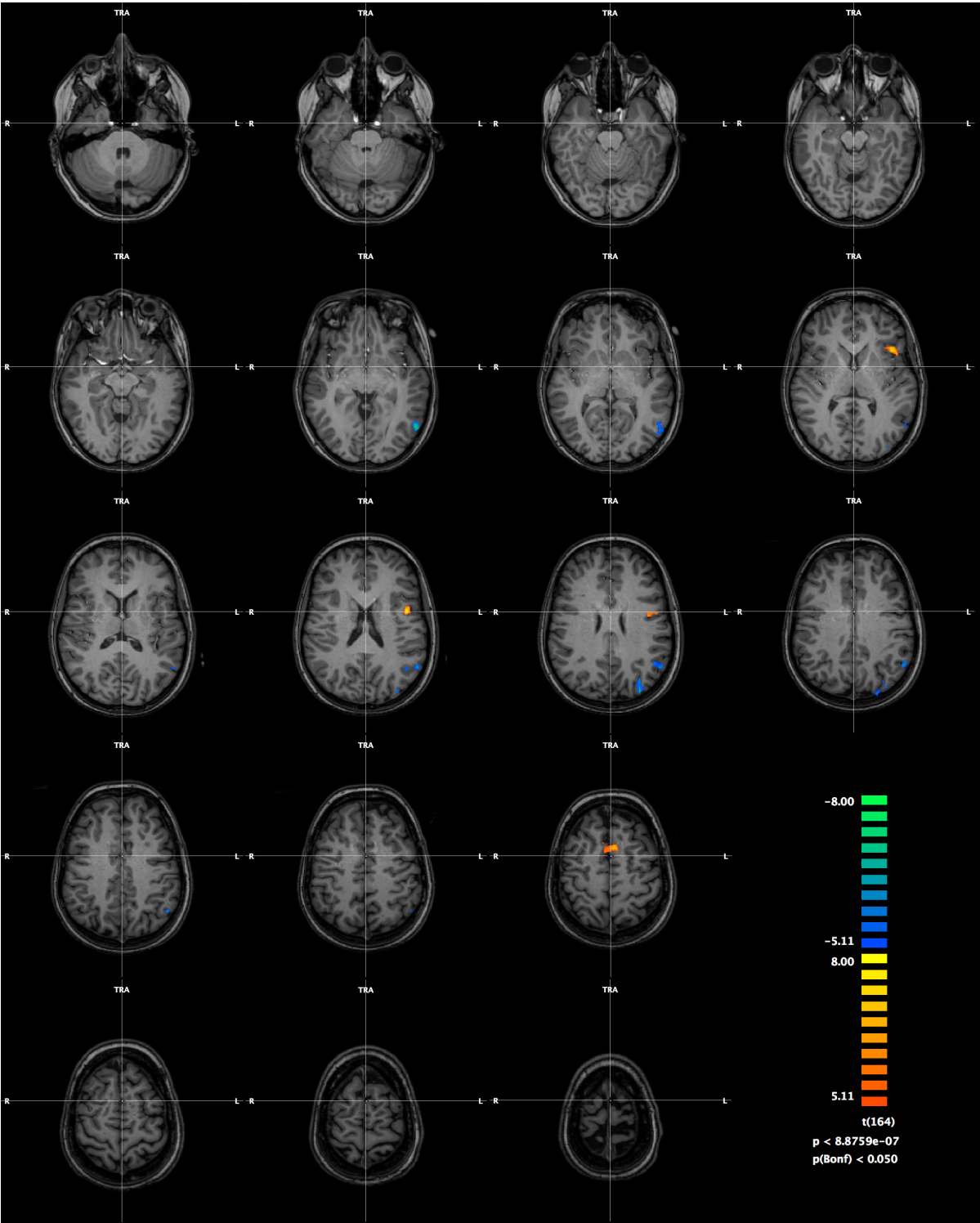
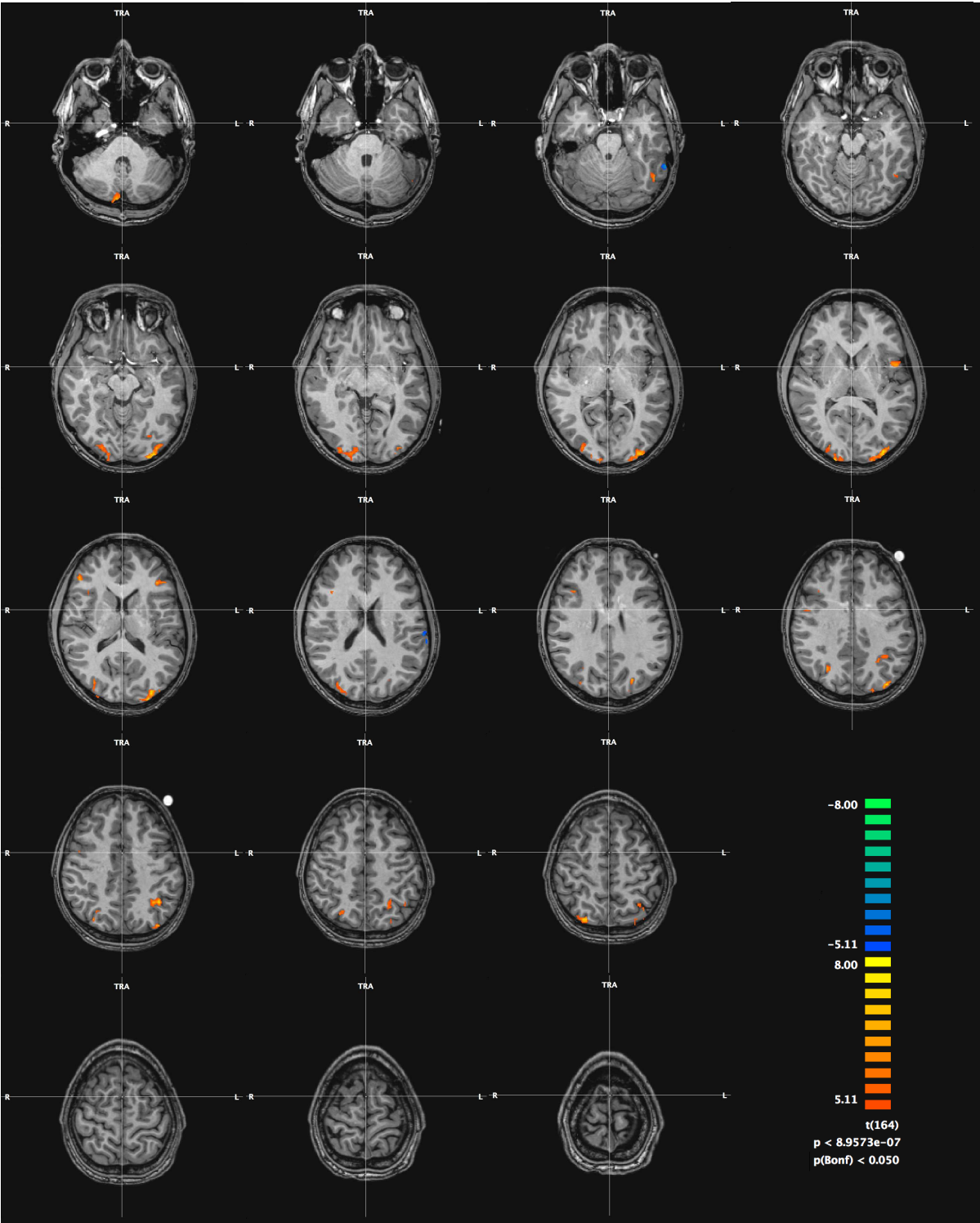**Orthographic reading (C04)**
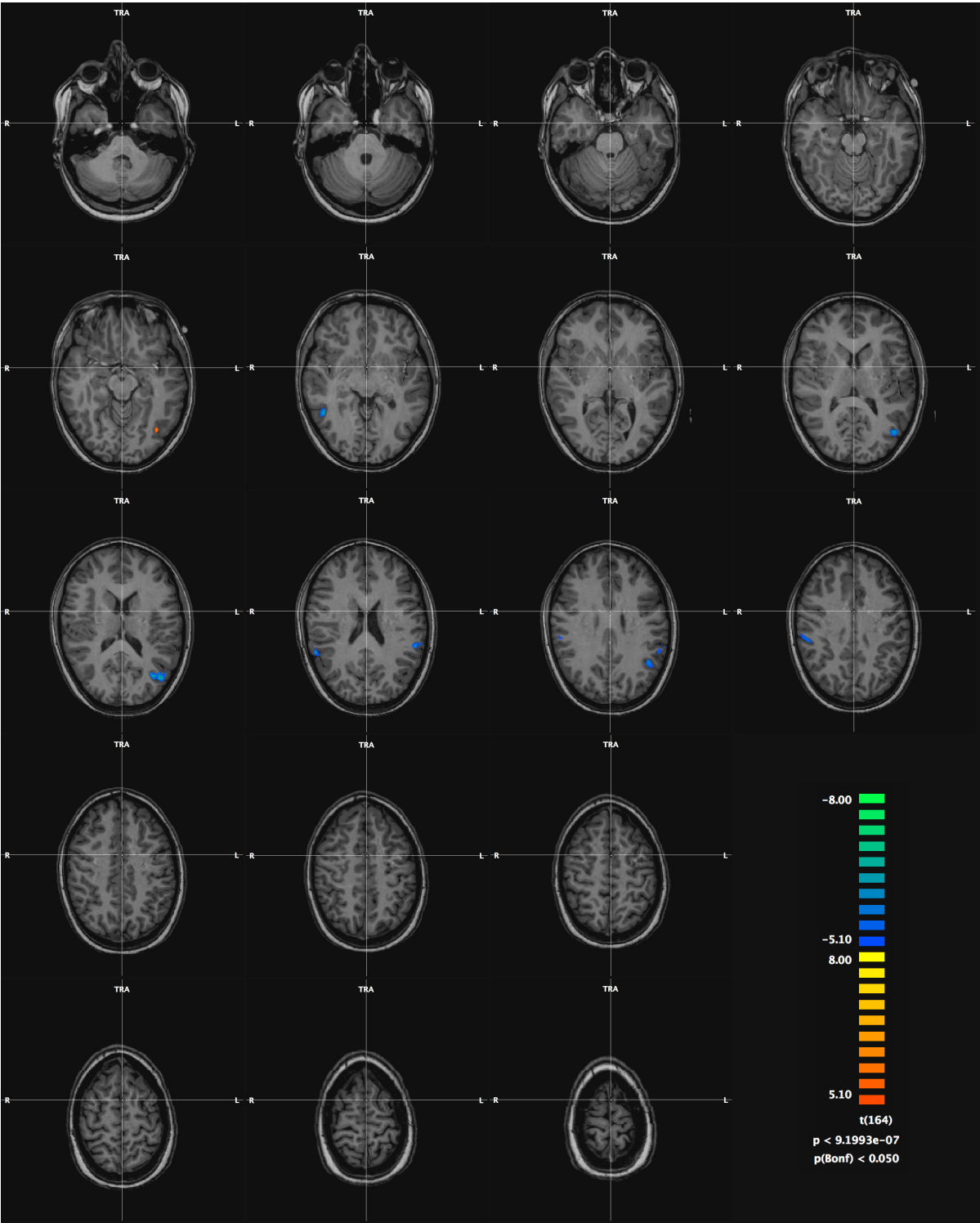
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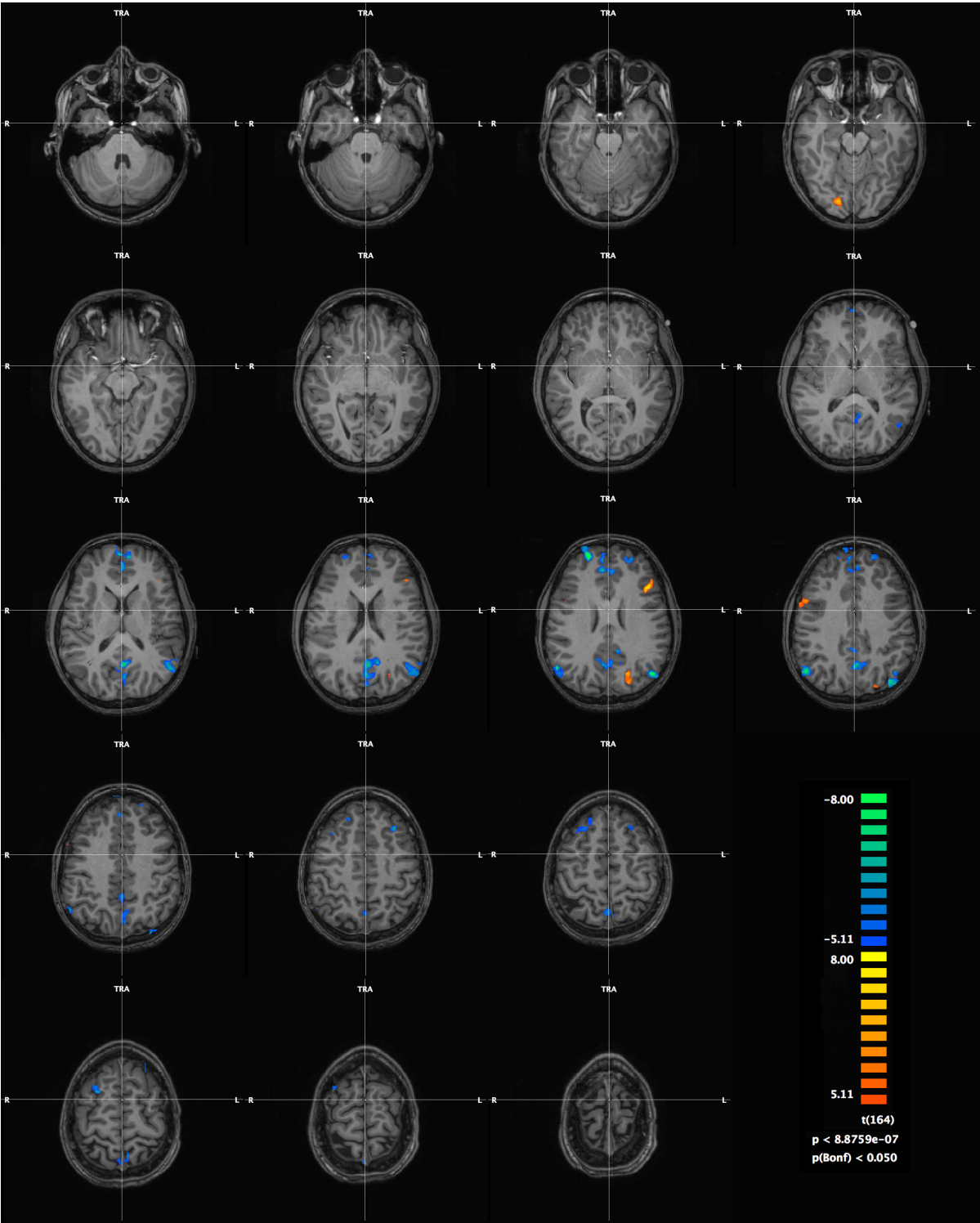
Orthographic reading (C06)
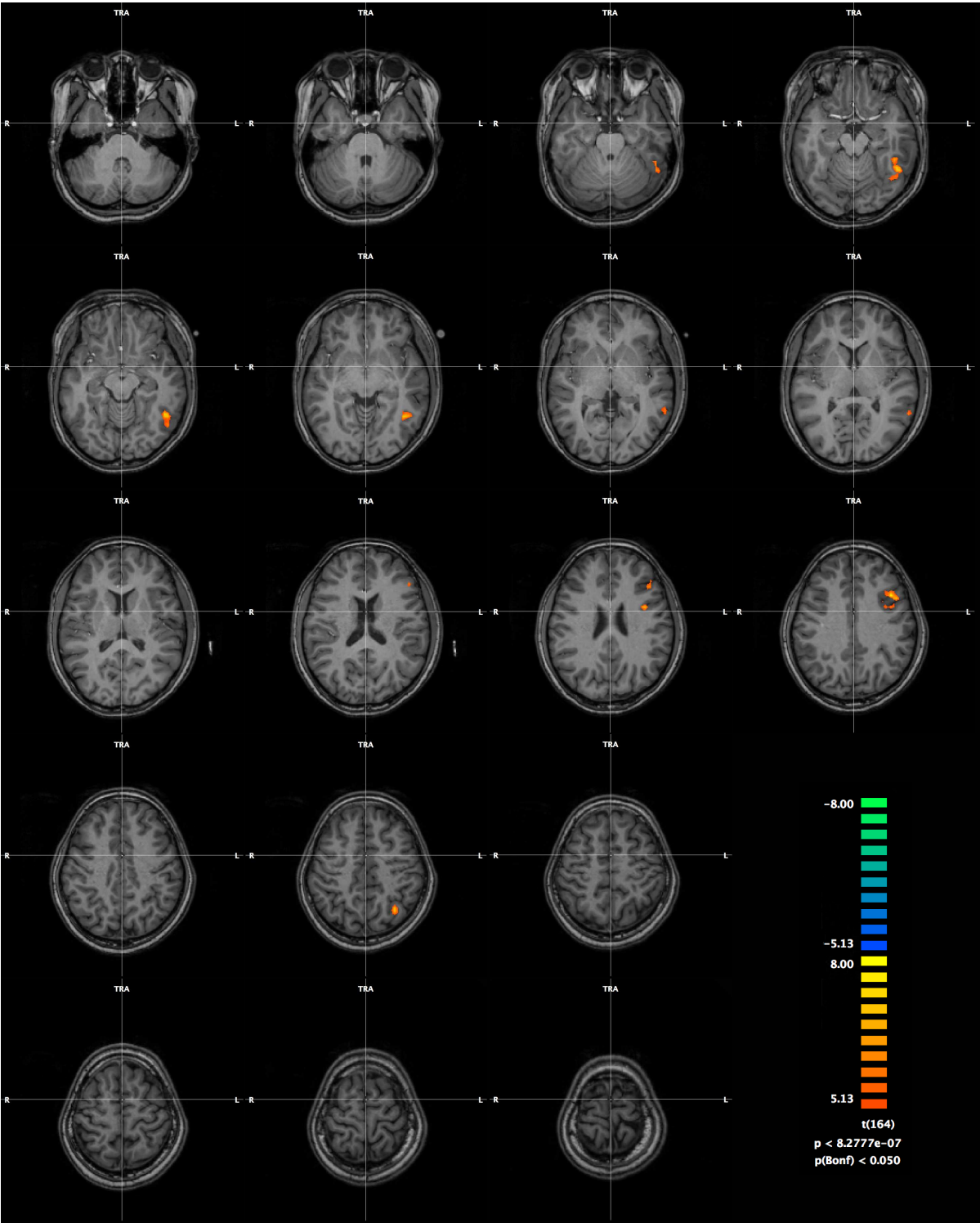
Orthographic reading (C09)
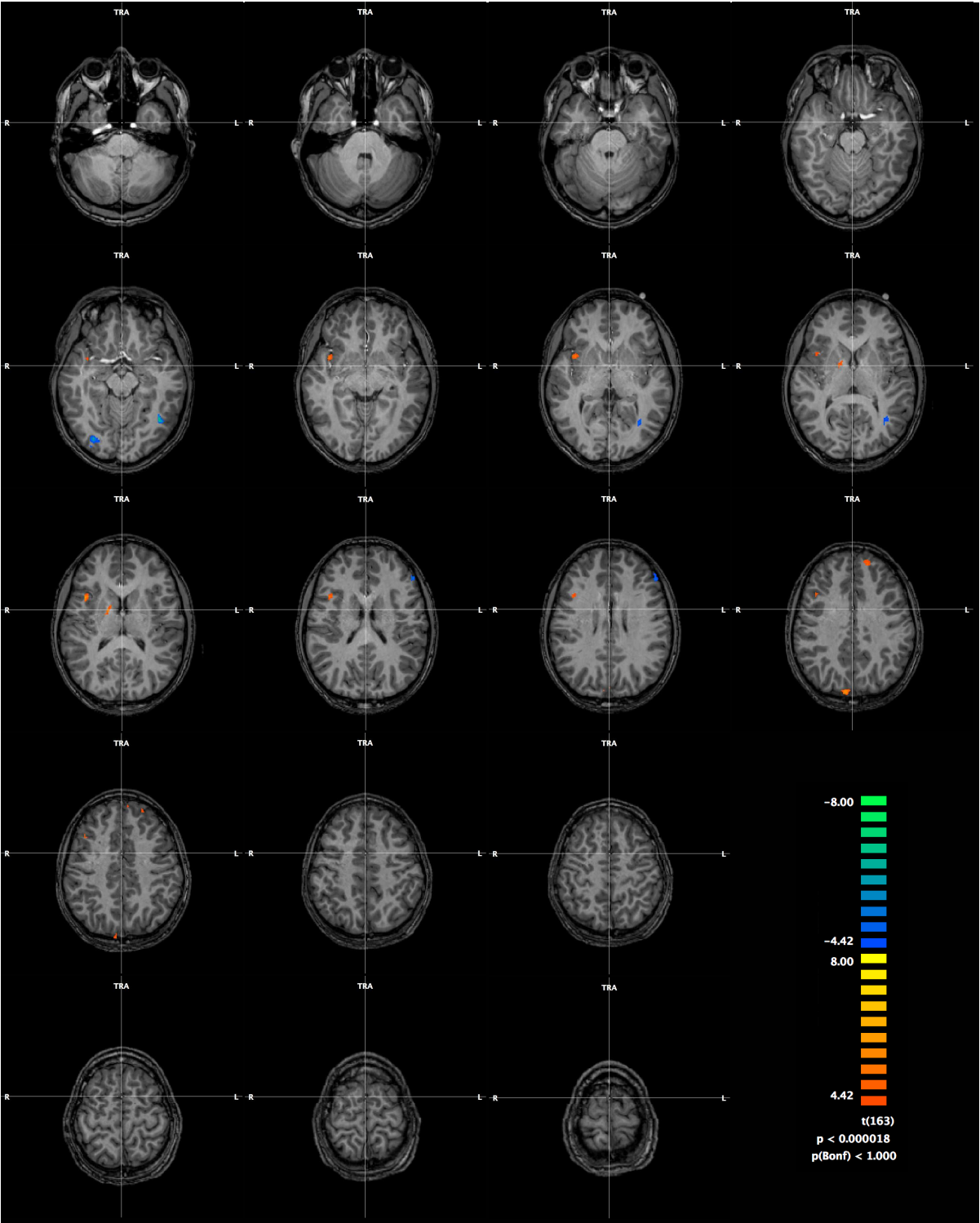
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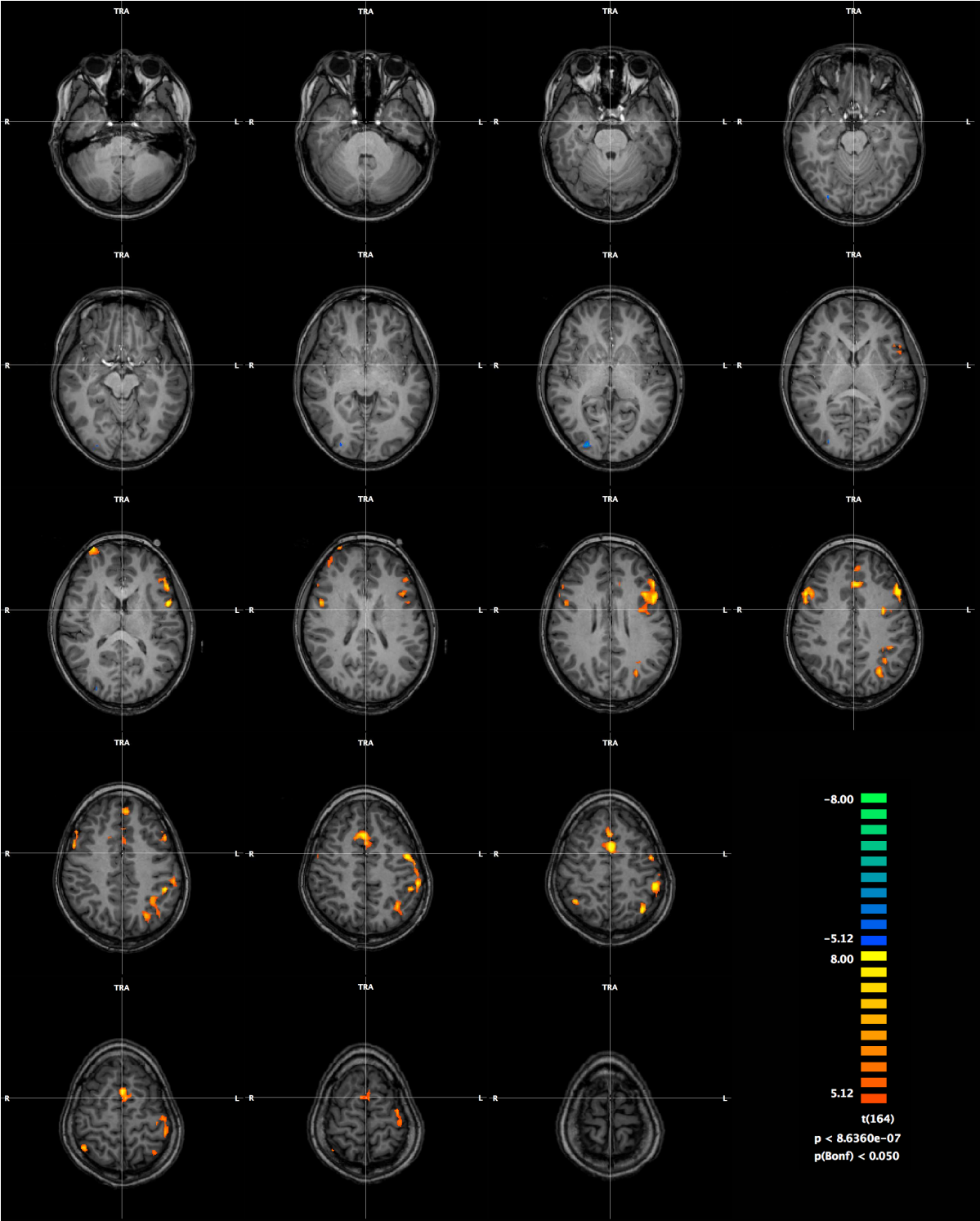
Orthographic reading (C12)
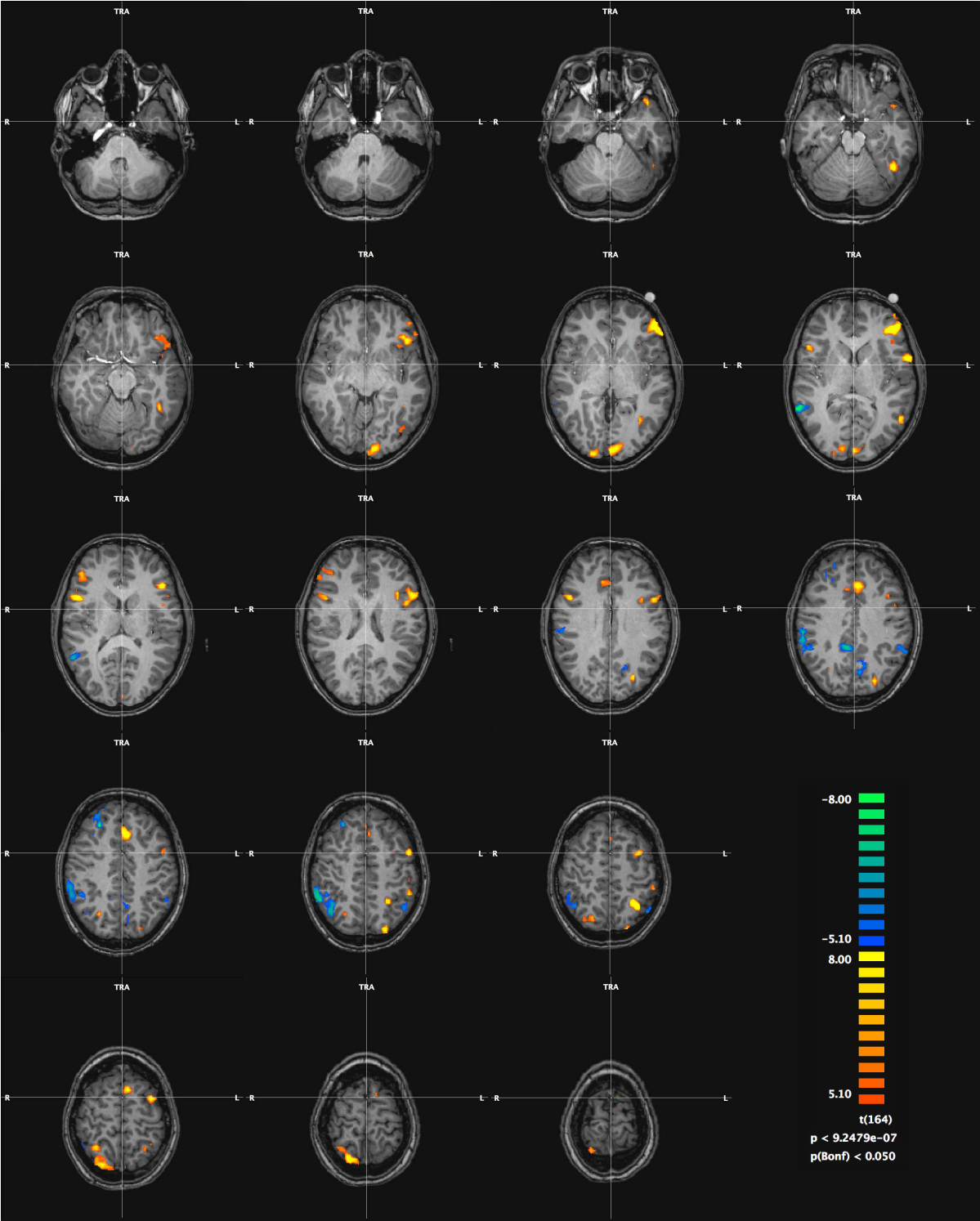
Orthographic reading (C14)
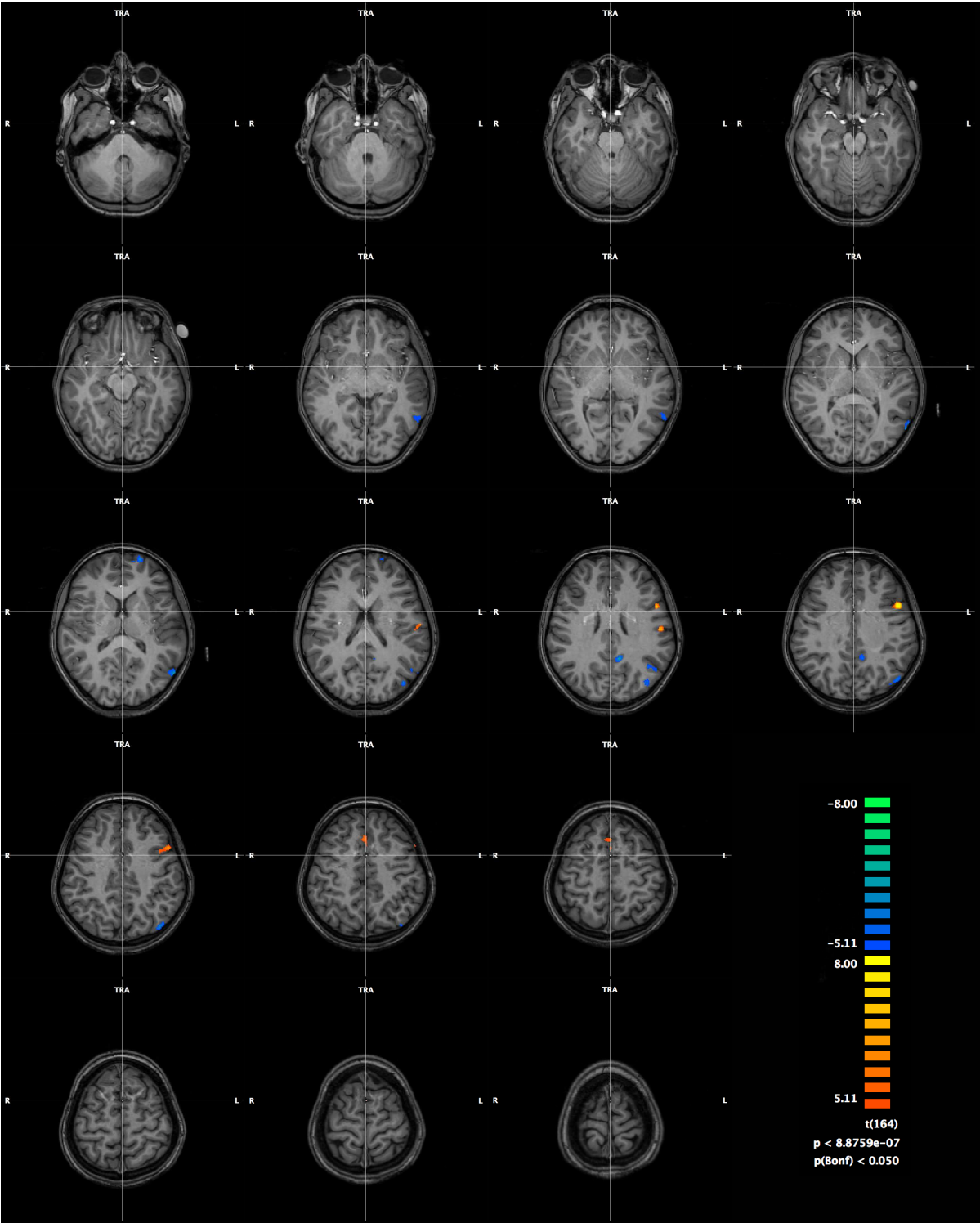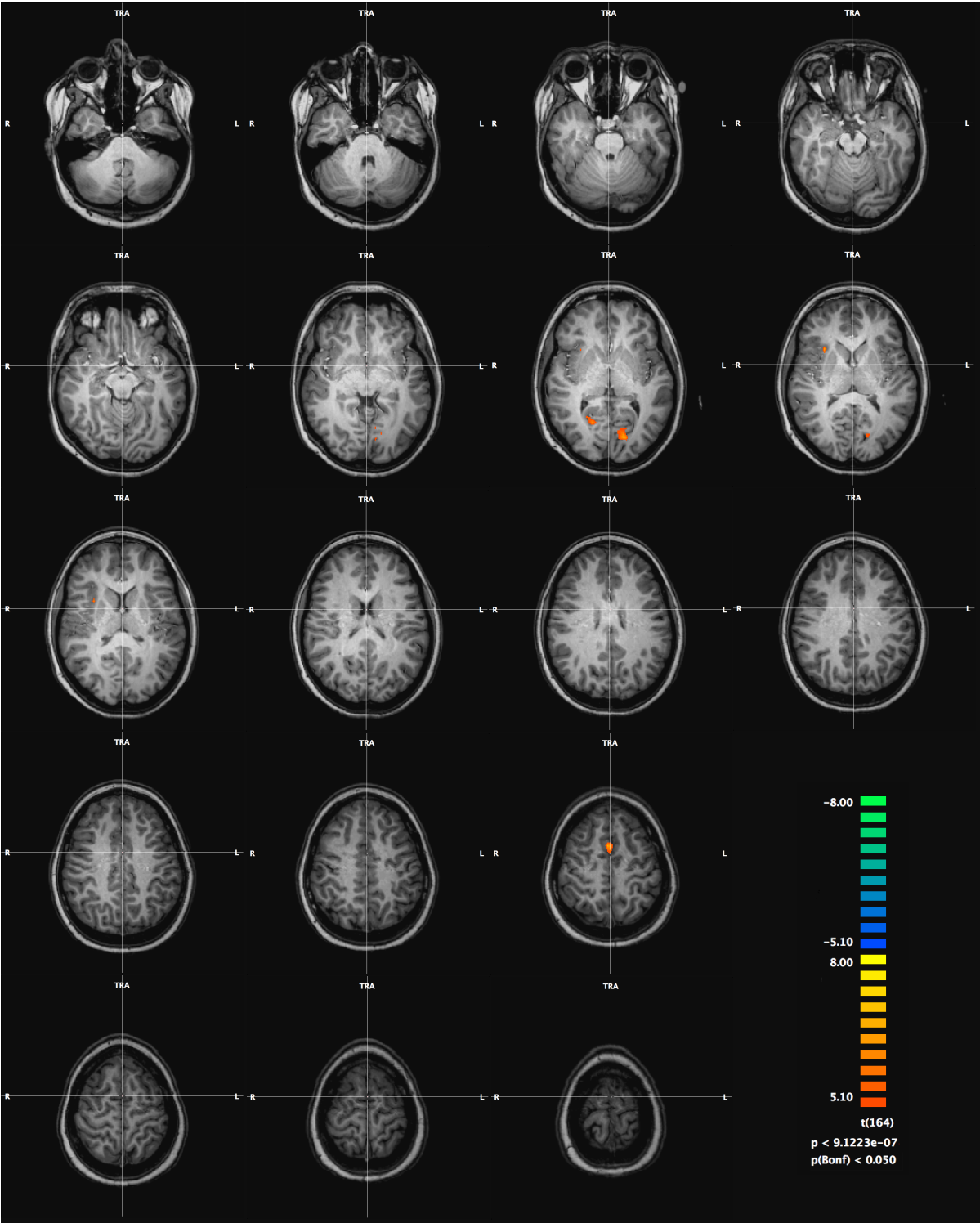
Orthographic reading (C15)
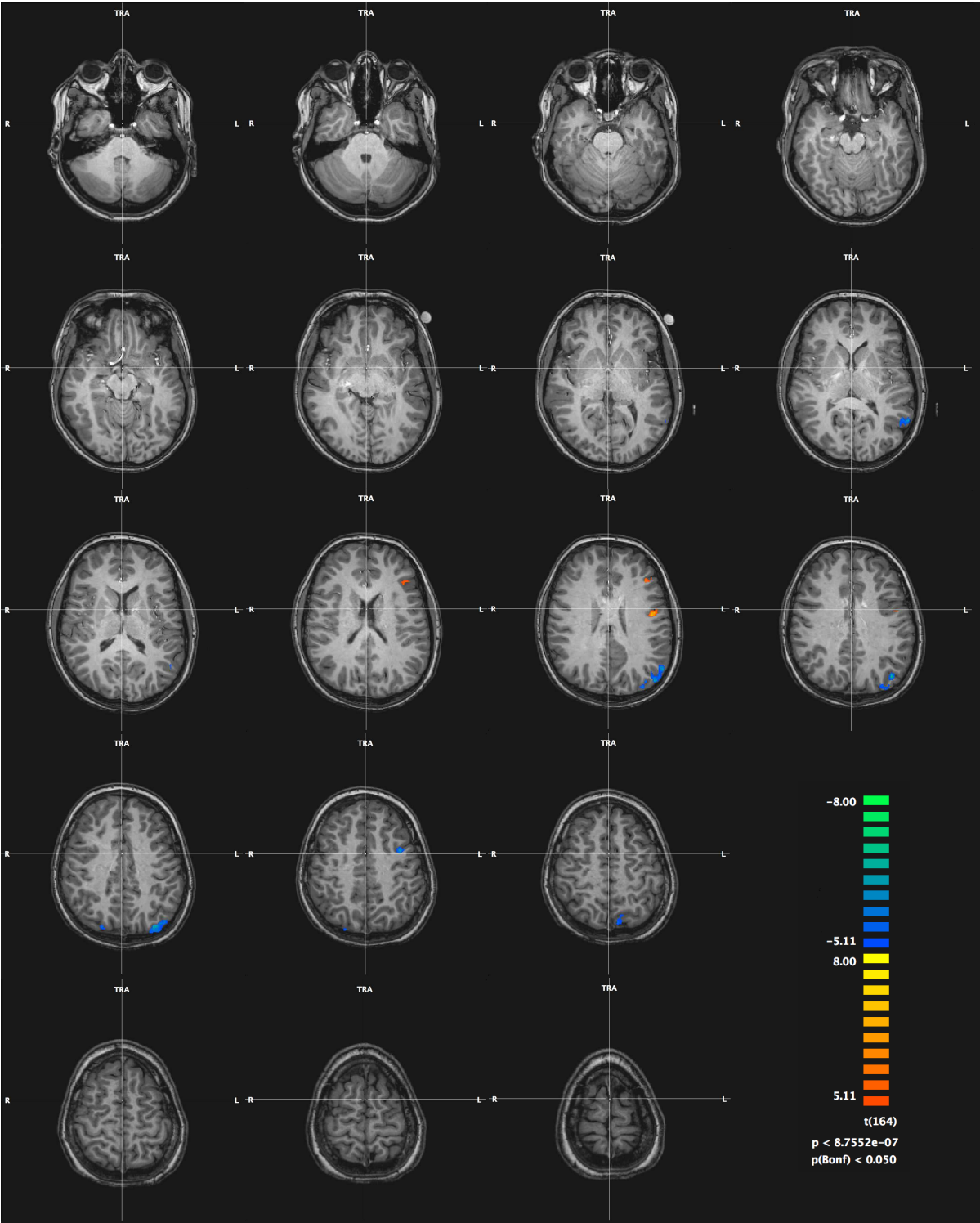
Orthographic reading (E01)
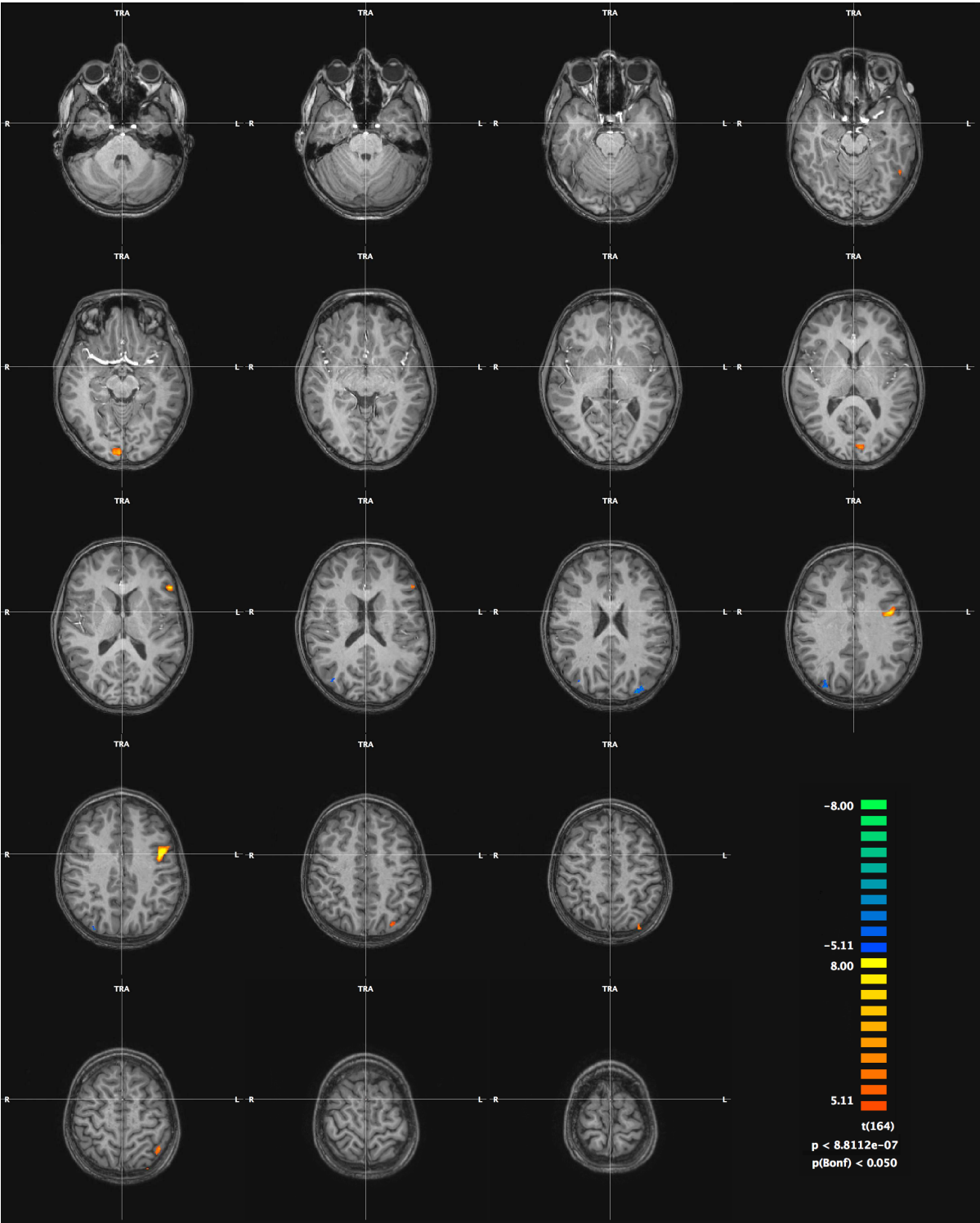
Orthographic reading (E02)
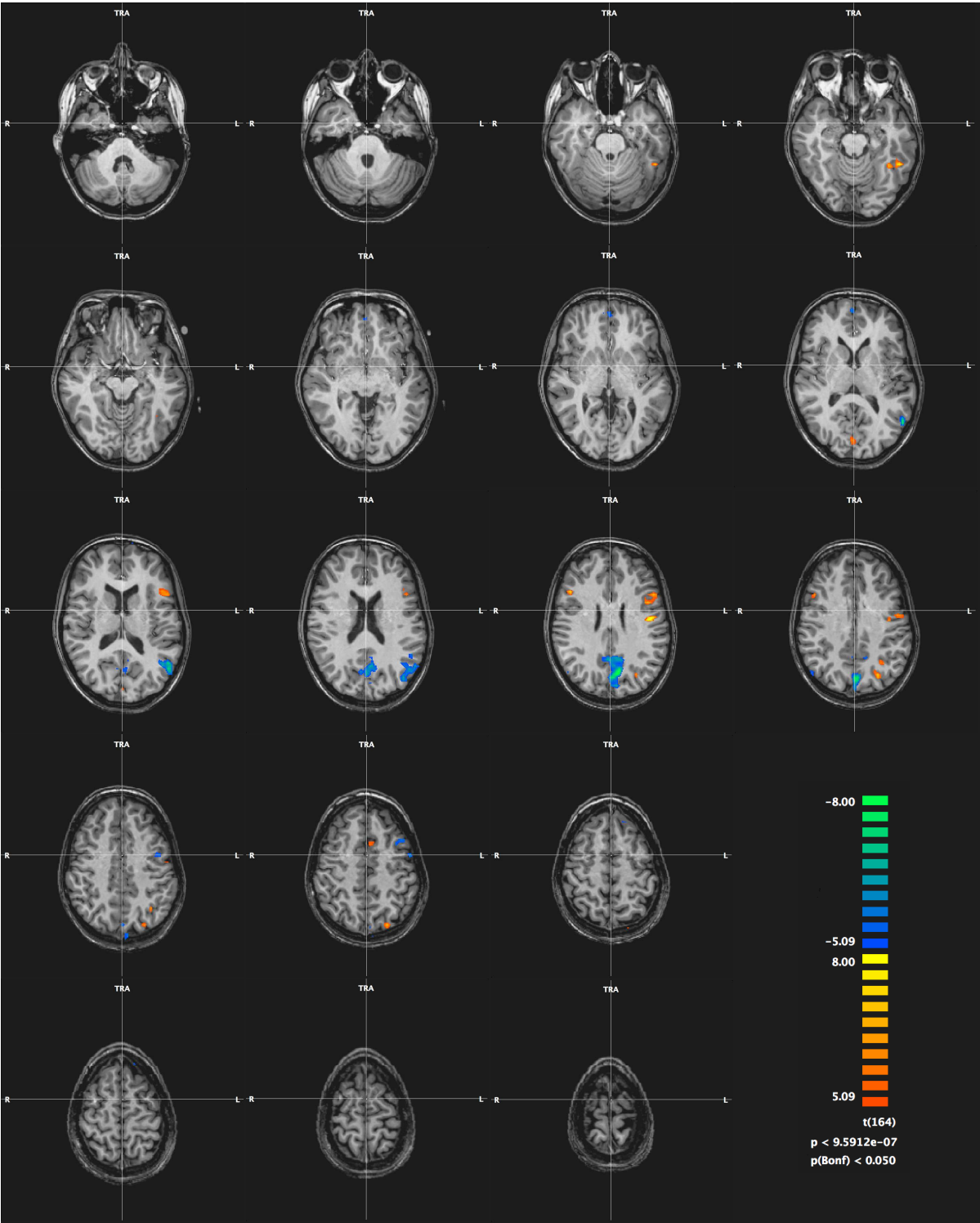
Orthographic reading (E05)

Orthographic reading (E17)

Appendix H: Individual ROIs utilized for regression analyses

Code [a]	Task	Hemis-phere	ROI [b]	Contrast [c]	Threshold [d]	Voxels (mm³)	Talairach coordinates (x, y, z)
C02	LOC	Left	LOC	Pics vs. scrambled	$p < .01$	506	(-33, -77, -7)
			LOC	Pics vs. scrambled	$p < .01$	534	(-32, -75, -23)
		Right	LOC	Pics vs. scrambled	$p < .01$	377	(39, -76, -13)
	Global motion	Left	MT	All vs. stationary	$p < .05$	488	(-33, -67, -9)
			Posterior MTG	85 vs. 0	$p < .05$	603	(-54, -51, -7)
			Trans occipital sulcus	85 vs. 0	$p < .05$	221	(-40, -63, 20)
		Right	MT	All vs. stationary	$p < .05$	528	(45, -65, -14)
			Trans occipital sulcus	85 vs. 0	$p < .05$	374	(50, -62, 14)
	Dichotic pitch	Left	Heschl's gyrus	All vs. silent	$p < .0001$	366	(-48, -15, 5)
			Heschl's gyrus	All vs. silent	$p < .0001$	597	(-43, -20, 5)
			Posterior STG	All vs. silent	$p < .0001$	493	(-52, -27, 13)
			Posterior STG	All vs. silent	$p < .0001$	761	(-36, -31, 11)
			Posterior STG	All vs. silent	$p < .0001$	652	(-43, -39, 12)
			Posterior STG	All vs. silent	$p < .0001$	717	(-53, -34, 12)
		Right	STG	All vs. silent	$p < .0001$	543	(52, -12, 6)
			Heschl's gyrus	All vs. silent	$p < .0001$	588	(44, -19, 7)
			Posterior STG	All vs. silent	$p < .0001$	610	(52, -23, 10)
			Posterior STG	All vs. silent	$p < .0001$	877	(37, -26, 9)
			Posterior STG	All vs. silent	$p < .0001$	487	(37, -35, 11)
C04	LOC	Left	LOC	Pics vs. scrambled	$p < .05$	850	(-37, -75, -10)
		Right	LOC	Pics vs. scrambled	$p < .05$	734	(36, -69, -6)
			LOC	Pics vs. scrambled	$p < .05$	704	(34, -75, 7)

Code [a]	Task	Hemisphere	ROI [b]	Contrast [c]	Threshold [d]	Voxels (mm³)	Talairach coordinates (x, y, z)
C04	Global motion	Left	MT	All vs. stationary	$p < .05$	411	(-36, -65, 3)
			MT	All vs. stationary	$p < .05$	537	(-36, -76, 7)
			Superior occ gyrus	All vs. stationary	$p < .05$	417	(-37, -77, 7)
		Right	MT	All vs. stationary	$p < .05$	326	(38, -62, 2)
			Inferior parietal	25 vs. 0	$p < .05$	210	(32, -66, 29)
			Superior parietal	25 vs. 0	$p < .05$	322	(16, -50, 61)
	Dichotic pitch	Left	Heschl's gyrus	All vs. silent	$p < .05$	400	(-43, -20, 4)
			Heschl's gyrus	All vs. silent	$p < .05$	389	(-38, -26, 5)
		Right	Heschl's gyrus	All vs. silent	$p < .01^{uncorr}$	346	(43, -19, 9)
C05	LOC	Left	LOC	Pics vs. scrambled	$p < .05$	350	(-43, -67, -11)
		Right	LOC	Pics vs. scrambled	$p < .05$	203	(38, -67, -15)
	Global motion	Left	MT	All vs. stationary	$p < .001$	552	(-38, -62, -5)
		Right	MT	All vs. stationary	$p < .001$	577	(43, -67, -11)
			MT	All vs. stationary	$p < .001$	383	(50, -53, 1)
			MT	All vs. stationary	$p < .001$	648	(43, -65, -4)
	Dichotic pitch	Left	Heschl's gyrus	All vs. silent	$p < .05$	342	(-45, -18, 2)
			Sylvian fissure	All vs. silent	$p < .05$	140	(-37, -35, 12)
		Right	Heschl's gyrus	All vs. silent	$p < .0001^{uncorr}$	295	(45, -18, 9)
			STG	All vs. silent	$p < .0001^{uncorr}$	253	(53, -9, 4)
			Posterior STG	All vs. silent	$p < .0001^{uncorr}$	379	(57, -26, 11)
C06	LOC	Left	LOC	Pics vs. scrambled	$p < .05$	267	(-43, -65, -4)
			LOC	Pics vs. scrambled	$p < .05$	322	(-39, -74, 3)
		Right	LOC	Pics vs. scrambled	$p < .05$	589	(43, -67, -2)
			LOC	Pics vs. scrambled	$p < .05$	339	(40, -76, -1)

Code [a]	Task	Hemis-phere	ROI [b]	Contrast [c]	Threshold [d]	Voxels (mm^3)	Talairach coordinates (x, y, z)
C06	Global motion	Left	MT	All vs. stationary	p < .05	571	(-42, -56, 7)
			MT	All vs. stationary	p < .05	628	(-46, -68, 3)
			Posterior STS	85 + 25 vs. 0	p < .05	288	(-41, -57, 21)
			Posterior STS	85 + 25 vs. 0	p < .05	222	(-33, -66, 33)
			Posterior STS	85 + 25 vs. 0	p < .05	170	(-41, -69, 23)
		Right	MT	All vs. stationary	p < .05	579	(39, -56, 9)
			MT	All vs. stationary	p < .05	531	(39, -68, 7)
			MT	All vs. stationary	p < .05	503	(46, -62, 9)
	Dichotic pitch	Left	Heschl's gyrus	All vs. silent	p < .05	283	(-45, -9, 7)
			Heschl's gyrus	All vs. silent	p < .05	685	(-44, -16, 13)
			STG	All vs. silent	p < .05	469	(-56, -16, 12)
		Right	Posterior STG	All vs. silent	p < .05	275	(54, -25, 15)
			Posterior STG	All vs. silent	p < .05	211	(55, -31, 13)
C09	LOC	Left	LOC	Pics vs. scrambled	p < .05	353	(-37, -78, -9)
		Right	LOC	Pics vs. scrambled	p < .05	330	(38, -81, 3)
			LOC	Pics vs. scrambled	p < .05	328	(39, -85, -10)
	Global motion	Left	MT	All vs. stationary	p < .001	448	(-44, -65, 2)
			Inferior parietal	85 + 25 vs. 0	p < .05	529	(-46, -73, 21)
		Right	MT	All vs. stationary	p < .001	585	(41, -60, -2)
	Dichotic pitch	Left	Heschl's gyrus	All vs. silent	p < .01^{uncorr}	374	(-44, -15, 12)
		Right	Heschl's gyrus	All vs. silent	p < .001^{uncorr}	232	(48, -15, 11)
C10	LOC	Left	LOC	Pics vs. scrambled	p < .001^{uncorr}	371	(-40, -73, -6)
		Right	LOC	Pics vs. scrambled	p < .001^{uncorr}	503	(43, -58, -14)

Code [a]	Task	Hemisphere	ROI [b]	Contrast [c]	Threshold [d]	Voxels (mm^3)	Talairach coordinates (x, y, z)
C10	Global motion	Left	MT	All vs. stationary	$p < .05$	433	(-37, -61, 0)
			Inferior parietal	85 + 25 vs. 0	$p < .05$	460	(-45, -65, 24)
			Inferior parietal	85 + 25 vs. 0	$p < .05$	494	(-38, -55, 23)
		Right	MT	All vs. stationary	$p < .05$	259	(39, -62, 1)
			Inferior parietal	85 vs. 0	$p < .05$	225	(42, -57, 20)
	Dichotic pitch	Left	STG	All vs. silent	$p < .0001^{uncorr}$	316	(-48, -25, 4)
			STG	All vs. silent	$p < .0001^{uncorr}$	165	(-37, -27, 11)
		Right	STG	All vs. silent	$p < .0001^{uncorr}$	310	(56, -18, 11)
			STG	All vs. silent	$p < .0001^{uncorr}$	113	(54, -29, 12)
C12	LOC	Left	LOC	Pics vs. scrambled	$p < .001^{uncorr}$	503	(-29, -75, -8)
			LOC	Pics vs. scrambled	$p < .0001^{uncorr}$	298	(-36, -60, -4)
		Right	LOC	Pics vs. scrambled	$p < .001^{uncorr}$	596	(31, -71, -6)
			LOC	Pics vs. scrambled	$p < .0001^{uncorr}$	455	(35, -63, -6)
	Global motion	Left	MT	All vs. stationary	$p < .001^{uncorr}$	186	(-43, -72, 8)
		Right	MT	All vs. stationary	$p < .001^{uncorr}$	517	(43, -66, 12)
			MT	All vs. stationary	$p < .001^{uncorr}$	304	(39, -74, 15)
	Dichotic pitch	Left	Heschl's gyrus	All vs. silent	$p < .05$	562	(-47, -15, 8)
			Heschl's gyrus	All vs. silent	$p < .05$	792	(-40, -21, 11)
			STG	All vs. silent	$p < .05$	571	(-52, -23, 10)
			Heschl's gyrus	All vs. silent	$p < .05$	491	(-35, -30, 13)
		Right	STG	All vs. silent	$p < .05$	419	(52, -11, 4)
			Heschl's gyrus	All vs. silent	$p < .05$	727	(40, -17, 9)
			STG	All vs. silent	$p < .05$	262	(58, -21, 10)

Code [a]	Task	Hemis-phere	ROI [b]	Contrast [c]	Threshold [d]	Voxels (mm^3)	Talairach coordinates (x, y, z)
C14	LOC	Left	LOC	Pics vs. scrambled	p < .00001	538	(-38, -78, -4)
			LOC	Pics vs. scrambled	p < .00001	821	(-38, -68, 0)
		Right	LOC	Pics vs. scrambled	p < .05	438	(35, -71, -9)
			LOC	Pics vs. scrambled	p < .05	570	(36, -62, -9)
	Global motion	Left	MT	All vs. stationary	p < .05	495	(-42, -77, 7)
			MTG	85 vs. 0	p < .05	212	(-45, -59, 0)
		Right	MT	All vs. stationary	p < .05	576	(40, -76, 1)
			MT	All vs. stationary	p < .05	679	(38, -71, 3)
	Dichotic pitch	Left	STG	All vs. silent	p < .05	465	(-51, -3, 5)
			Heschl's gyrus	All vs. silent	p < .05	606	(-44, -17, 9)
			Posterior STG	All vs. silent	p < .05	798	(-56, -18, 8)
			Sylvian fissure	All vs. silent	p < .05	426	(-38, -29, 14)
		Right	Heschl's gyrus	All vs. silent	p < .05	309	(47, -2, 2)
			Heschl's gyrus	All vs. silent	p < .05	645	(47, -10, 5)
C15	LOC	Left	LOC	Pics vs. scrambled	p < .05	356	(-47, -76, -6)
			LOC	Pics vs. scrambled	p < .05	239	(-39, -69, -7)
		Right	LOC	Pics vs. scrambled	p < .05	361	(40, -63, -12)
	Global motion	Left	MT	All vs. stationary	p < .05	253	(-49. -69, 8)
		Right	MT	All vs. stationary	p < .01^{uncorr}	476	(37, -66, 1)
	Dichotic pitch	Left	STG	All vs. silent	p < .05	569	(-53, -20, 9)
			Heschl's gyrus	All vs. silent	p < .05	171	(-40, -27, 10)
		Right	Heschl's gyrus	All vs. silent	p < .01^{uncorr}	437	(47, -16, 5)

Code [a]	Task	Hemis-phere	ROI [b]	Contrast [c]	Threshold [d]	Voxels (mm³)	Talairach coordinates (x, y, z)
E01	LOC	Left	LOC	Pics vs. scrambled	p < .05	232	(-39, -74, -13)
			LOC	Pics vs. scrambled	p < .05	192	(-35, -72, -8)
			LOC	Pics vs. scrambled	p < .05	155	(-42, -62, -17)
		Right	LOC	Pics vs. scrambled	p < .05	277	(28, -76, -6)
			LOC	Pics vs. scrambled	p < .05	439	(35, -71, -10)
			LOC	Pics vs. scrambled	p < .05	423	(38, -69, -12)
	Global motion	Left	MT	All vs. stationary	p < .05	395	(-42, -64, 0)
			MT	85 + 25 vs. 0	p < .01^{uncorr}	321	(-38, -62, 4)
		Right	MT	All vs. stationary	p < .05	278	(38, -65, 3)
			Inferior parietal	85 vs. 25	p < .01^{uncorr}	574	(34, -61, 18)
	Dichotic Pitch	Left	STG	All vs. silent	p < .05	338	(-53, -12, 12)
			Heschl's gyrus	All vs. silent	p < .05	397	(-44, -19, 11)
		Right	Heschl's gyrus	All vs. silent	p < .05	502	(51, -14, 12)
			Posterior STG	All vs. silent	p < .05	226	(60, -20, 19)
E02	LOC	Left	LOC	Pics vs. scrambled	p < .001	377	(-42, -67, -13)
			LOC	Pics vs. scrambled	p < .001	433	(-37, -76, -10)
		Right	LOC	Pics vs. scrambled	p < .001	428	(36, -62, -15)
			LOC	Pics vs. scrambled	p < .001	222	(37, -72, -8)
	Global motion	Left	MT	All vs. stationary	p < .05	505	(-37, -68, -3)
		Right	MT	All vs. stationary	p < .05	383	(39, -66, 1)
	Dichotic pitch	Left	STG	All vs. silent	p < .05	334	(-56, -13, 6)
			Heschl's gyrus	All vs. silent	p < .05	528	(-45, -16, 4)
			Heschl's gyrus	All vs. silent	p < .05	298	(-37, -25, 4)

Code [a]	Task	Hemis-phere	ROI [b]	Contrast [c]	Threshold [d]	Voxels (mm³)	Talairach coordinates (x, y, z)
E02	Dichotic pitch	Right	Heschl's gyrus	All vs. silent	$p < .05$	315	(53, -7, -1)
			Posterior STG	All vs. silent	$p < .05$	624	(60, -17, 8)
			Posterior STG	All vs. silent	$p < .05$	618	(55, -27, 9)
E05	LOC	Left	LOC	Pics vs. scrambled	$p < .0001^{uncorr}$	275	(-38, -73, -16)
			LOC	Pics vs. scrambled	$p < .0001^{uncorr}$	231	(-42, -59, -16)
		Right	LOC	Pics vs. scrambled	$p < .0001^{uncorr}$	246	(36, -70, -17)
	Global motion	Left	MT	85 vs. 0	$p < .0001$	502	(-46, -67, -3)
			Superior parietal	85 vs. 0	$p < .0001$	329	(-26, -69, 49)
		Right	MT	85 vs. 0	$p < .0001$	499	(44, -62, 4)
			Superior parietal	85 vs. 0	$p < .0001$	430	(26, -69, 44)
	Dichotic pitch	Left	STG	All vs. silent	$p < .01^{uncorr}$	112	(-52, -14, 7)
		Right	STG	All vs. silent	$p < .01^{uncorr}$	128	(53, -11, 7)
E17	LOC	Left	LOC	Pics vs. scrambled	$p < .000001$	363	(-44, -71, -12)
			LOC	Pics vs. scrambled	$p < .00001$	389	(-41, -74, 7)
			LOC	Pics vs. scrambled	$p < .0001$	320	(-44, -66, -14)
		Right	LOC	Pics vs. scrambled	$p < .000001$	486	(41, -73, 0)
			LOC	Pics vs. scrambled	$p < .000001$	240	(45, -72, 8)
			LOC	Pics vs. scrambled	$p < .00001$	354	(45, -62, -12)
	Global motion	Left	MT	All vs. stationary	$p < .01^{uncorr}$	195	(-47, -62, 11)
		Right	MT	All vs. stationary	$p < .05$	222	(41, -56, 8)
	Dichotic pitch	Left	Heschl's gyrus	All vs. silent	$p < .05$	308	(-44, -16, 9)
			STG	All vs. silent	$p < .10$	116	(-58, -12, 6)
		Right	Heschl's gyrus	All vs. silent	$p < .10$	134	(49, -14, 9)

Appendix H (continued)

Notes:
[a] Participant codes:

        C = control average reader

        E = experimental dyslexic reader

[b] Regions of interest:

        LOC = lateral occipital cortex

        MT = middle temporal

        MTG = middle temporal gyrus

        Occ = occipital

        STG = superior temporal gyrus

        STS = superior temporal sulcus

        Trans = transverse

[c] Possible contrasts for each task:

        LOC (unscrambled pictures vs. scrambled pictures)

        Global motion (all moving dots vs. stationary dots; 85% vs. 25%; 85% vs. 0%; 25% vs. 0%; 85% and 25% vs. 0%)

        Dichotic pitch (all auditory conditions vs. silent; SBR 10 vs. SBR 1; SBR 10 vs. SBR 0; SBR 1 vs. 0; SBR 10 and 1 vs. 0)

        If contrast type is not listed for a ROI, this was not visible in whole-brain analyses.

[d] Thresholds shown as Bonferroni-corrected *p*-values, unless otherwise stated by 'uncorr' which denotes uncorrected *p*-values.

Appendix I: UBC Research Ethics Board Certificates of Approval

ETHICS CERTIFICATE OF MINIMAL RISK APPROVAL: RENEWAL

PRINCIPAL INVESTIGATOR:	DEPARTMENT:	UBC C&W NUMBER:
Deborah E. Giaschi	UBC/Medicine, Faculty of/Ophthalmology & Visual Science	H07-01723

INSTITUTION(S) WHERE RESEARCH WILL BE CARRIED OUT:

Institution	Site
UBC	Vancouver (excludes UBC Hospital)
Children's and Women's Health Centre of BC (incl. Sunny Hill)	Child & Family Research Institute

Other locations where the research will be conducted:
Fraser Academy 2294 West 10th Avenue Vancouver, BC V6K 2H8 www.fraser-academy.bc.ca

CO-INVESTIGATOR(S):

L. Leigh Field
Dorothy Edgell
Marita Partanen
Bruce Bjornson

SPONSORING AGENCIES:

- British Columbia Ministry of Children and Family Development - "Neurobiology of reading and temporal processing deficits in developmental dyslexia"
- Canadian Language and Literacy Research Network (CLLRNet) - Networks of Centres of Excellence (NCE) - "The neurobiology and genetics of temporal processing deficits in Dyslexia"

PROJECT TITLE:
The Neurobiology and Genetics of Temporal Processing Deficits in Dyslexia

REMINDER: The current UBC Children's and Women's approval for this study expires: September 17, 2010

APPROVAL DATE: September 17, 2009

CERTIFICATION:
In respect of clinical trials:
1. The membership of this Research Ethics Board complies with the membership requirements for Research Ethics Boards defined in Division 5 of the Food and Drug Regulations.
2. The Research Ethics Board carries out its functions in a manner consistent with Good Clinical Practices.
3. This Research Ethics Board has reviewed and approved the clinical trial protocol and informed consent form for the trial which is to be conducted by the qualified investigator named above at the specified clinical trial site. This approval and the views of this Research Ethics Board have been documented in writing.

The Chair of the UBC Children's and Women's Research Ethics Board has reviewed the documentation for the above named project. The research study, as presented in the documentation, was found to be acceptable on ethical grounds for research involving human subjects and was approved for renewal by the UBC Children's and Women's Research Ethics Board.

Approved by one of:

Dr. Marc Levine, Chair   Dr. Mason Bond, Associate Chair

Appendix I (continued)

Sep 17 2009

C&W Institutional Certificate of Approval
-- RENEWAL --

PRINCIPAL INVESTIGATOR Giaschi, Deborah E.	DEPARTMENT Ophthalmology	NUMBER CW07-0171 / H07-01723

CO-INVESTIGATORS:
Bjornson, Bruce; Field, L. Leigh; Edgell, Dorothy; Partanen, Marita;

C&W DEPARTMENTS, PATIENT BASED PROGRAMS AND ADMINISTRATIVE JURISDICTIONS IMPACTED BY THIS STUDY:
Acute and Critical Care;

SPONSORING AGENCIES:
Canadian Language and Literacy Research Network (CLLRNet) - Networks of Cen; BC Ministry of Children and Family Development;

TITLE
The Neurobiology and Genetics of Temporal Processing Deficits in Dyslexia

TERMS OF RENEWAL
Sep 17 2009 - Sep 16 2010

CERTIFICATION:

Ethical approval has been granted for the above-referenced research project. I am pleased to inform you that all necessary hospital program/resource approvals and institutional agreements/contracts are now in place and that you have permission to begin your research.

_____
Dr. Stuart MacLeod
Vice President, Academic Liaison and Research Coordination,
Provincial Health Services Authority

This Certificate of Approval is valid for the above term provided there is no change in the research protocol