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The origins of cortical multisensory dynamics: Evidence from human infants

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ABSTRACT

Classic views of multisensory processing suggest that cortical sensory regions are specialized. More recent views argue that cortical sensory regions are inherently multisensory. To date, there are no published neuroimaging data that directly test these claims in infancy. Here we used fNIRS to show that temporal and occipital cortex are functionally coupled in 3.5-5-month-old infants (N = 65), and that the extent of this coupling during a synchronous, but not an asynchronous, audiovisual event predicted whether occipital cortex would subsequently respond to sound-only information. These data suggest that multisensory experience may shape cortical dynamics to adapt to the ubiquity of synchronous multisensory information in the environment, and invoke the possibility that adaptation to the environment can also reflect broadening of the computational range of sensory systems.

1. Introduction

Multisensory processing is critical to perception and attention (Amso and Scerif, 2015; Macaluso et al., 2016) and to complex learned skills, including speech production and language comprehension (Bishop and Miller, 2009; Rosenblum, 2008; Skipper et al., 2007). Until recently, the classic view of multisensory processing has been that cortical regions are inherently specialized, for example sound information is only processed in temporal cortex (see Macaluso, 2006 for review). In this view, multisensory processing only occurs when modality-specific information reaches higher-order association areas. This view has been challenged by the alternative that the neocortex is largely a multisensory organ (Ghazanfar and Schroeder, 2006). This newer view is based on several strands of evidence. First, occipital and temporal cortices have been found to respond to both auditory and visual stimulation in adults (see Murray et al., 2016 for review). Second, multisensory interactions occur not only in higher-order association areas, but also and concurrently in the midbrain and in sensory-specific cortices (Stein and Stanford, 2008). Finally, multisensory interactions in sensory cortical areas occur as early as 40 ms following sensory input, suggesting that feedforward mechanisms from low-level sensory regions are as likely to support multisensory processing as feedback from higher-level association cortex (Foxe and Schroeder, 2005; Schroeder and Foxe, 2005).

What remains unclear is the developmental origin of these effects. To our knowledge, there are no cortical neuroimaging studies in human infants that have uniquely tested the inherent versus experience-dependent origins of multisensory processing. This is despite the fact that infants begin life with powerful, though relatively rudimentary, behavioral multisensory processing abilities (Lewkowicz and Ghazanfar, 2009; Lewkowicz, 2014). For instance, infants use temporal synchrony to perceive multisensory coherence from birth (Lewkowicz et al., 2010; Lewkowicz, 1996, 2010), as well as to support learning in general (Bahrick and Lickliter, 2000). The relevancy of synchrony for multisensory processing is evident at the neural level in adult findings. For instance, prior work has shown that synchronous multisensory experience drives functional connectivity among occipital and temporal cortices, which then enhances unisensory processing (Lewis and Noppeney, 2010; Tyll et al., 2013). Yet, the bulk of the data on multisensory processing in the brain comes from adult data, and, unfortunately, those data reflect the bias of years of exclusive exposure to synchronous multisensory experiences. Thus, a consensus about the inherent or experience-driven multisensory nature of cortex cannot be assumed from adult data because they represent a far more mature developmental state.

Prior work examining multisensory processing using neuroimaging in infancy was not designed to determine the unisensory or multisensory nature of cortex and, indeed, offers conflicting evidence on this issue. For example, Bortfeld et al. (2007) used fNIRS to examine 6-9month-old infants' occipital and temporal responses to visual animations either in isolation or when paired with speech sounds. They found that left temporal cortex activation was specific to speech sounds and

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that occipital cortex was specific to the visual animations. Similarly, Taga and Asakawa (2007) presented 2-4-month-old infants with speech sounds in alternation with checkerboard patterns. They found that visual events do not affect unrelated auditory processing in infancy. In contrast, other studies using fNIRS have shown that presentation of audiovisual information increases activation in both areas relative to when the sound was removed (Watanabe et al., 2013; Emberson et al., 2015). These findings indicate that occipital cortex may be multisensory because it responds in an additive fashion to the audio + visual information. Finally, it has been found that 5-month-old infants have event related potentials associated with more efficient stimulus processing when exposed to synchronous as opposed to asynchronous audiovisual events (Reynolds et al., 2014). Although important, these results do not provide any insights into the effects of short-term experience on multisensory processing. In other words, no studies to date have directly measured infant neural responses to unisensory information before and after a multisensory experience and whether such experience can induce changes in the cortical dynamics underlying sensory processing.

Thus, while there is evidence for multisensory processing in temporal and occipital regions by adulthood, data about the developmental origins of these cortical dynamics are controversial. Our work addresses this gap in the literature by examining the role of short-term synchronous and asynchronous multisensory experience in shaping cortical sensory processing in 3.5-5-month-old infants. This age range was chosen because infants only begin to integrate audiovisual information without the use of low-level cues, such as temporal synchrony, starting around 6-8 months of age (Lewkowicz and Röder, 2012). Thus, examining individual differences in younger infants, who have greater variability in multisensory processing, allows for mechanistic insight into the cortical dynamics that may support this developmental shift. We used fNIRS to measure the functional response patterns of occipital and temporal cortical regions to unisensory sound and visual stimuli. Critically, measurements were made before and after infants experienced the same stimuli as part of synchronous and asynchronous multisensory audiovisual familiarization events (Fig. 1). We predicted one of three results. First, the occipital and/or temporal regions might be unisensory, but functionally connected such that they bind or integrate the sound and visual signals in Synchronous but not in Asynchronous familiarization events. This finding would suggest early specialization of cortical sensory function but correlated activity in the two cortices in support of multisensory integration. Second, temporal cortex and/or occipital cortex might be multisensory and respond to both sound and visual signals. Finally, occipital and temporal regions might be functionally connected during Synchronous but not Asynchronous familiarization events and, as a result, might train each otherwise unisensory region to become multisensory. This last finding would suggest that multisensory integration observed in adults reflects an emergent, experience-driven developmental process.

2. Method

2.1. Participants

The final sample included N = 65 3.5-5-month-old infants (*M* age = 134.2 days, *SD* = 12.1 days; 31 females, 34 males, 48 white non-Hispanic, 4 black, 9 Hispanic, and 4 Asian). The X University Institutional Review Board approved the study procedure and parental consent was obtained prior to testing. Infants were recruited from department of health birth records. We prescreened for premature birth (< 36 weeks), very low birth weight (< 5 lb), or health problems. An additional 20 infants were tested but excluded because of fussiness (n = 14), poor optical contact with the scalp (n = 5), or parental interference (n = 1).

2.2. Design & procedure

Participants sat on a parent's lap in a dimly-lit room approximately 60 cm away from a 22" monitor. Stimuli were presented via E-Prime software. Visual stimuli were a red or green ball (2.3° visual angle) presented on a rectangular grid of white dots (17° by 14.3°) on a black background (Fig. 1). The ball moved back-and-forth across the grid horizontally or vertically at a rate of 2.5 s per motion cycle (i.e., return to starting position). Auditory stimuli were two sounds ("bang" and "boing"). Associations between the visual stimulus and the sound it was paired with were counterbalanced. Using a block design, three blocks of 20-s events were presented. Each event was preceded by a 10-s white fixation cross on a black background.

Fig. 1 illustrates block order. In the first block, we administered two 20-s pretest events: a Visual-only event in which the ball was presented without sound, and a Sound-only event in which the sound was presented at 2.5-s intervals (the grid of white dots was presented on the screen but without a moving ball). These events were designed to measure baseline responses to unisensory information. Pretest event order was counterbalanced.

Next, we presented the *Synchronous* and *Asynchronous* blocks, each of which consisted of a 20-s familiarization event followed by a 20-s Visual-only test event and a 20-s Sound-only test event. During the familiarization event, the ball moved either up and down or back and forth across the screen for eight cycles or trials, and the sound was presented eight times. The sound was presented as the ball reached the edge of the grid and changed directions in the Synchronous event, whereas during the Asynchronous event the sound was presented 450 ms before the ball reached the edge. The subsequent Visual-only and Sound-only test events were identical to the Pretest block events. The order of the Synchronous and Asynchronous blocks and the order of Visual-only and Sound-only test events were counterbalanced across infants. Infants' looking behavior was coded offline by a trained observer.

2.3. fNIRS recording

fNIRS recordings were collected at a rate of 50 Hz using a TechEn CW6 system with eight channels (two sources and eight detectors). Source optodes emitted infrared light at two frequencies, 690 nm and 830 nm, which are optimized to measure deoxygenated and oxygenated blood, respectively. The fNIRS channels were arranged in two arrays, each with one source optode and four detector optodes (Fig. 2). Sourcedetector separation was 3 cm. The lateral/temporal array (channels T1-4) was positioned in the cap so that the detector optodes were centered over EEG coordinate T4 (right superior/middle temporal lobe) and the posterior array (channels O1-4) was positioned so that the detector optodes were centered over EEG coordinate O2 (right middle/inferior occipital lobe) (anatomical correlates of international 10-20 system coordinates obtained from Kabdebon et al., 2014). This positioning aligns with the 10-20 coordinates used for localizing occipital and temporal activation in prior fNIRS work with infants (e.g., Emberson et al., 2015; Bortfeld et al., 2007). The cap was placed on infants' heads such that the bottom of the cap aligned with the Fp1-Fpz-Fp2 line. The arrays were always positioned on the right hemisphere due to constraints on the number of optodes available.

2.4. Data preprocessing

2.4.1. fNIRS data processing

fNIRS data were exported and preprocessed in the HOMER2 v2.1 MATLAB toolbox. Data were digitally band-pass filtered at 0.01-0.1 Hz to remove systematic physiological and movement artifacts. The change in optical density was then calculated for each wavelength relative to the 10 s baseline prior to block onset. Changes in the concentration of oxygenated and deoxygenated hemoglobin were calculated from the

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