

RUNNING HEAD: VISUAL-TACTILE CO-LOCATION IN INFANTS

Perception of visual-tactile co-location in the first year of life

Livia Freier^{1,3}, Luke Mason^{1,2}, & Andrew J. Bremner¹

¹Sensorimotor Development Research Unit, Department of Psychology, Goldsmiths,
University of London

³Department of Cognitive, Linguistic, and Psychological Science, Brown University

²Centre for Brain and Cognitive Development, Birkbeck, University of London

ACCEPTED FOR PUBLICATION IN *DEVELOPMENTAL PSYCHOLOGY* (APRIL 2016)

<http://www.apa.org/pubs/journals/dev/> Copyright APA (This article may not exactly replicate the final version published in the APA journal. It is not the copy of record.)

KEYWORDS: Multisensory development; Infancy; Perceptual development; Touch; Spatial cognitive development; Body representation

ABSTRACT WORD COUNT: 144 (MAX = 250); WORD COUNT: 4283

ACKNOWLEDGEMENTS: This research was supported by an award from the European Research Council under the European Community's Seventh Framework Programme (FP7/2007-2013) (ERC Grant agreement no. 241242) to AJB. Additional support for the write-up of this article was provided by the European Union Seventh Framework Programme (FP7/2007-2013) (Grant agreement no. 289404). The authors would like to thank the parents and infants who took part in the study.

CORRESPONDENCE TO: Professor Andrew J. Bremner, Department of Psychology, Goldsmiths University of London, SE14 6NW. United Kingdom; Tel. +44 (0) 207 078 5142; email: a.bremner@gold.ac.uk.

ABSTRACT

An ability to perceive tactile and visual stimuli in a common spatial frame of reference is a crucial ingredient in forming a representation of one's own body and the interface between bodily and external space. In this study we investigated young infants' abilities to perceive co-location between tactile and visual stimuli presented on the hands. We examined infants' visual preferences for spatially congruent and incongruent visual-tactile events across two age groups (6-months and 10-month). We observed increased duration of looking to incongruent stimuli displays in both age groups, indicating that infants from at least 6 months of age demonstrate the ability to determine whether simultaneously presented visual-tactile perceptual events are co-located or not. These findings indicate that an ability to perceive visual and tactile stimuli within a common spatial frame of reference is available by the end of the first half year of life.

A paradigmatic question for philosophers and developmental scientists alike concerns whether human infants are able to perceive space amodally – i.e., whether they can build a common representation of space independent of the particular input modality (e.g., Eilan, 1993; Meltzoff, 1993). Research with human adults and animals has shown that when (and when not) stimuli to different sense modalities originate from a common location in external space, this has important implications for neural processing and behaviour (e.g., Meredith & Stein, 1996; Stein & Stanford, 2008; Spence & Driver, 2004; Wallace, Roberson, Hairston, Stein, Vaughan, & Schirillo, 2004). Adults perceive and make use of spatial commonalities across the senses in a seemingly effortless manner. However, given the substantial differences between adults and infants in the degree and quality of their multisensory experience we cannot assume that infants possess the same ability to represent multisensory space.

It is now common to argue that spatial properties of the environment (e.g., shape and place) number among a range of “amodal” sensations which are specified in a redundant manner across modalities (e.g., Bahrick & Lickliter, 2000; Gibson, 1969; Walker-Andrews, 1994). Developmental scientists have been by no means idle when it comes to addressing the question of how infants and young children develop in their ability to perceive such aspects of the multisensory environment (for a recent review see Bahrick & Lickliter, 2012; although note that there is some disagreement concerning what counts as an amodal property, Lewkowicz & Kraebel, 2004). However, multisensory perceptual development has been primarily investigated via investigations of infants’ learning about crossmodal temporal relations (typically in the auditory and visual modalities). For instance, it has been demonstrated that an ability to detect audiovisual synchrony and intensity (loudness matched with brightness) emerges early in infancy (e.g., Bahrick, 1992; Bahrick, Flom & Lickliter,

2002; Lewkowicz, 1996; Lewkowicz, 2000; Lewkowicz & Turkewitz, 1980; Spelke, 1976). Similarly it has been suggested that synchrony between sound and vision (Lewkowicz, Leo, & Simion, 2010), and vision and touch (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013) may be readily perceived from the moment of birth, with even some crossmodal temporal links available prenatally in some non-human species such as bobwhite quails (Jaime, Bahrick, & Lickliter, 2010).

Investigations of the development of an ability to perceive spatial commonalities across the senses are less frequent in the literature. Some studies suggest that very young infants can notice whether or not sounds and sights are co-located in external space, but such findings have not always been easy to replicate (e.g., Aronson & Rosenbloom, 1971; McGurk & Lewis, 1974; Morrongiello, Fenwick, & Chance, 1998). Scant research has examined infants' abilities to detect and represent common spatial aspects of visual-tactile stimulation. This is surprising given the importance of linking visual and tactile events for the development of a coherent perception of the body and the embodied environment (Bremner & Cowie, 2013). Research efforts in this area have focused primarily on infants' recognition of shapes and textures of objects across unimodal presentations (crossmodal transfer tasks; see Streri, 2012), and generally support the notion that the ability to match shape and texture between tactile and visual modalities is an early acquired skill (e.g., Abravanel, 1981; Bryant, Jones, Claxton, & Perkins, 1972; Rose, 1994), that is even present in newborns albeit in a limited way (e.g., Sann & Streri, 2007; Streri & Gentaz, 2003, 2004). However, because the spatial matches in crossmodal transfer tasks are "field independent", they do not require an ability to locate features within a common spatial frame of reference, and therefore do not indicate whether infants perceive such multisensory events in an external (or even a peripersonal) spatial environment (e.g., Bremner & Cowie, 2013; Eilan, 1993).

One way to investigate the extent to which participants can coordinate representations of space across the senses is via crossmodal orienting responses. Visual orienting responses to sounds have been reported in newborns (e.g., Butterworth & Castillo, 1976; Wertheimer, 1961) although with an extended developmental trajectory throughout the first months (Clifton, Morrongiello, Kulig, & Dowd, 1981; Muir & Field, 1979). Whilst both reflexive orienting of the head to touch (e.g., Fényes, Gergely, & Tóth, 1960; Sherrington, 1910; Zappella & Simopoulos, 1966) and habituation of head turning to touch (e.g., Moreau, Helfgott, Weinstein, & Milner, 1978) have been reported, oculomotor responses to tactile events are surprisingly infrequent in young infants. Bremner, Mareschal, Lloyd-Fox, & Spence (2008) investigated visual orienting to vibrotactile stimuli in 6- and 10-month-olds by presenting stimuli unpredictably to each hand. Only the 10-month-olds in this study were able to consistently orient towards the stimulated location, indicating that the ability to coordinate visual and tactile frames of reference undergoes significant development throughout the first year of life.

In many ways it seems unsurprising that infants may struggle to translate between visual and tactile frames of reference as, in computational terms, this is not a trivial problem. Adult humans and primates are equipped with neural circuits that continuously update correspondences between visual and tactile spatial frameworks across changes in posture (e.g., Azañón & Soto-Faraco, 2008; Graziano, Gross, Taylor, & Moore, 2004; Lloyd, Shore, Spence, & Calvert, 2002; Rigato, Bremner, Mason, Pickering, Davis, & Van Velzen, 2013). Indeed, as a result of eye movements, these computational challenges also impinge on our ability to detect co-location between visual and auditory stimuli (Pöppel, 1973). Research with infants indicates that an ability to incorporate information about posture into sensory processing develops gradually across the first year of life (e.g., Bremner et al., 2008; Rigato,

Begum Ali, Van Velzen, & Bremner, 2014), and continues even into early childhood (e.g., Begum Ali, Cowie, & Bremner, 2014; Pagel, Heed, & Röder, 2009). It is especially pertinent to the current investigation that these challenges posed by variations in body and limb posture are particularly complex across ontogenetic development. Not only do the relative sizes and shapes of the limbs, body, and head change rapidly even from day to day (Lampl, Veldhuis, & Johnson, 1992) but, additionally, the number and variety of postural changes which an infant can readily and spontaneously execute become increasingly complex with age (e.g., Van Hof et al., 2002).

As outlined above, infants do not easily locate unimodal tactile stimuli via visual orienting responses until 10 months of age (Bremner et al., 2008). This may be explained by the extended development up to 10 months of age of an ability to take account of posture when locating tactile stimuli (Bremner et al., 2008; Rigato et al., 2014). Thus, the ability to perceive tactile and visual stimuli within a common external spatial frame of reference may develop slowly in the first year, implying a state of tactile solipsism in the first months of life. However, no research has yet investigated the development of an ability to register visual-tactile co-location in early infancy. Indeed, it is possible that the presence of a distinct visual stimulus (which was not present to guide the crossmodal orienting responses to tactile stimuli studied by Bremner et al., 2008) may aid infants in determining the spatial frame of reference within which to locate a tactile stimulus. Thus, we investigated the ability to perceive visual-tactile spatial co-location in 6- and 10-month-old infants.

--Insert Figure 1 about here--

We investigated whether infants would show a spontaneous visual preference for spatially congruent or incongruent visual-tactile stimulus pairs presented on the hands. Infants' looking behaviour was compared in response to two sets of stimulus combinations

(see Fig. 1): (1) an incongruent condition in which visual and tactile stimuli were presented concurrently on different hands, and (2) a congruent condition in which the visual and tactile stimuli were presented together on the same hand. Stimuli in both congruent and incongruent presentations always alternated between hands. This step was taken in order to prevent influences on looking behaviour from proximal aspects of the stimulation (e.g., a preference for visual stimuli on the right hand). Because the only variation between conditions concerns the common or separate locations of visual and tactile stimuli within an external frame of reference, a spontaneous visual preference for either display implies an ability to detect co-location across vision and touch.

Method

Design

We examined whether infants showed a visual preference for trials in which visual and tactile stimuli appeared on the same hand or for trials in which they appeared together on different hands. Each trial consisted of ten consecutive bimodal stimuli in which visual flashes on the back of the hand and vibrotactile stimuli on the palm were presented in synchrony (both onset and offset were synchronised). Each of these ten bimodal stimuli was presented for 700 ms with 1500 ms interstimulus intervals between them (see Fig. 1), and thus each trial lasted 20.5 seconds. During congruent trials the bimodal stimuli were presented on one hand at a time, alternating between left and right hand. Thus visual and tactile stimuli were always co-located on congruent trials. During the incongruent trials the visual and vibrotactile stimuli were presented synchronously on different hands. All participants were presented with two blocks of trials, with each block comprising two trials: one incongruent and one congruent. The order of condition was the same across block for

each participant, and the starting condition for each block was counterbalanced across participants and age groups.

Participants

The final sample was made up of 24 infants. Twelve 6-month-old infants (4 male, 8 female, $M = 196.6$ days, $SD = 5.6$) comprised the younger group, and 12 10-month-olds comprised the older group (6 male, 6 female, $M = 315.1$ days, $SD = 5.9$). All infants were full-term and had no known medical conditions or developmental complications. An additional 13 infants were tested (five 6-month olds and eight 10-month-olds), but were excluded from the data analysis as they did not complete a minimum of four experimental trials due to fussiness (4), excessive movement, which interfered with the testing procedure (6) and parental interference, which may have biased looking preferences (3). The experiment was run in accordance with APA ethical principles for conducting research with children, and ethical approval was granted from the institutional Research Ethics Committee. Informed consent was obtained before testing was initiated and parents and legal guardians received a short debrief afterwards. Parents and legal guardians were naïve concerning the experimental hypotheses of the study.

Apparatus and stimuli

All testing took place in a dimly lit room in which infants were seated on their parents' laps with their hands placed on a small table (337 cm x 20 cm) directly in front of them. Vibrotactile devices ("tactors") were placed into the infants' palms, fixed in place with cohesive bandage and covered with cotton mittens. The tactors were voice coil transducers, which generated vibrotactile stimulation when driven at 220 Hz by a sinusoidal pure tone. The visual stimuli were provided by two light emitting diodes (LEDs), which were attached, one to each of the mittens positioned such that they were clearly visible on the back of the

infants' hands. The tactors and LEDs were controlled via an EPRIME 1.1 script (Psychology Software Tools, Pittsburgh, PA), operating custom-built parallel port controlled stimulus presentation hardware. The infants' looking behaviour was recorded via a single infrared camera, which was located opposite the infant's body midline.

Procedure

The infants were seated upright on their parents' laps with both arms held by an experimenter from across the small table in front of them. This experimenter immediately began to attract the infants' attention by engaging them in a game that directed their gaze towards the back of their hands. The first experimental block began as soon as the infants looked at their hands, and the experimenter, ensuring that the infants' hands were comfortably within their visual field, had crouched out of the infant's sight behind the table. All stimulus presentations were triggered by a second experimenter, who was monitoring the infant's looking behavior from an adjacent room via a live video feed. This experimenter further ensured that the infant looked at his/her hands prior triggering a trial. Between trials, the experimenter outside of the room signalled to the experimenter in the test room (by means of intercom) whether the infant's attention needed to be redirected towards their hands. On this cue, the experimenter in the test room redirect the infant's attention towards the back of their hands and a new trial began. The experimenter in the test room who held the infants' hands at the wrist, was unable to detect any of the presented visual-tactile stimuli. The recorded video files were coded offline. Each recorded trial was coded frame by frame, and the onset and offset of each gaze directed towards the hands (either the lit or the unlit hand) was used to calculate the duration of looking at both hands across each trial. A second observer, who was not aware of the purpose of the study, coded 20% of randomly selected

recordings. The inter-observer reliability for looking time, estimated by the interclass correlation between coders was high (.96, $F(7, 7) = 29.19, p < .001$).

Results

Preliminary analyses revealed no significant main effects and interactions of Gender and Order of trial presentations. These factors were thus excluded from further analysis. Figure 2 illustrates the mean looking times per trial across blocks and age groups. The means indicate a looking preference for the incongruent trials (over the congruent trials) across blocks and age groups. We examined the reliability of these effects using a 2 x 2 mixed analysis of variance (ANOVA) of infants' looking durations per trial with the within-participants factor Congruency (Congruent / Incongruent), and the between-participants factor Age group (6-month-olds / 10-month-olds). A main effect of Congruency, $F(1, 22) = 31.7, p < .001, \eta_p^2 = .59$, confirmed a looking preference for the incongruent ($M = 8555$ ms, $SD = 4064$) over the congruent stimulus presentations ($M = 6356$ ms, $SD = 3713$). No other main effect or interaction reached statistical significance.

--Insert Figure 2 about here--

Given the relatively small sample size obtained, null effects in the above analysis should be treated with some caution. Particular care should be taken with the null interaction of Congruency x Age group, $F(1, 22) = 2.8, p = .103, \eta_p^2 = .12$. Given the sample size, a medium effect size of 0.69 would be required of this interaction in order to achieve a power of 0.8, and so smaller interactions may have been missed. Thus, we ran further t-tests in order to confirm that the effect of Congruency was present in each age group. Significantly longer looking at the incongruent than the congruent displays was confirmed at both 10 [$t(11) = 7.1, p < .001, d_z = 1.93$] and 6 [$t(11) = 2.3, p = .043, d_z = 0.66$] months of age.

Discussion

An ability to perceive co-location across visual and tactile events is crucial to forming representations of spatial relationships between the body and our external surroundings (Eilan, 1993). Previous research investigating the ability to coordinate visual and tactile space has only looked at crossmodal visual orienting to tactile stimuli (Bremner et al., 2008). Here we assessed the perception of visual-tactile co-location in 6- and 10-month-old infants using a visual preference paradigm in which both tactile and visual stimuli were presented simultaneously. Results indicate that infants of both age groups demonstrate a spontaneous visual preference for spatially separate over co-located visual and tactile stimuli presented to their hands. Thus, infants are sensitive to spatial co-location between visual and tactile cues from at least 6 months of age, and before they are able to orient visually to tactile stimuli presented in isolation (Bremner et al., 2008)

On first consideration it may seem unsurprising that 6-month-olds, who are generally able to grasp and haptically explore objects, also demonstrate an ability to recognise whether tactile and visual stimuli originate from a single spatial location. Indeed, infants and even newborns show emerging abilities to map tactile to visual patterns in crossmodal transfer tasks (e.g., Bryant et al., 1976; Rose, 1994; Streri, 2012). However, it is our contention that an ability to perceive co-location among sense modalities is a more complex attainment than recognising a spatial pattern across modalities. Co-locating tactile and visual stimuli on the hands requires infants to locate each stimulus with respect to a common frame of reference which is neither exclusively related to sensory or to external frames of reference (Bremner et al., 2008). As such, evidence of sensitivity to visual-tactile co-location is more indicative of an ability to represent sensory information with regard to the external world (Eilan, 1993) and the interface between the body and the external world (Bremner et al., 2008).

It is pertinent to ask why, if 6-month-old infants can coordinate tactile and visual frames of reference in co-locating visual and tactile stimuli, researchers have so far failed to demonstrate that infants of this age are able to visually orient to tactile stimuli on the hands. Bremner et al. (2008) find that this is not present at 6 months but develops by 10 months of age. There are a range of differences between the procedure used by Bremner et al. (2008), and that used in the current study which might explain the different ages at which infants demonstrated competence. However, our preferred explanation is that the visual stimuli which we presented in the current study (and which were not presented in Bremner et al., 2008) bootstrapped the young infants' ability to locate the tactile stimuli in external (visual) space. It is possible that an ability to visually orient to a tactile stimulus in the absence of any distinct visual locational cue requires a more detailed representation of crossmodal spatial relations than noticing the broader scale differences between the crossmodally congruent and incongruent stimulus events presented in the current experiment. As infants gain more experience of visual-tactile events across the first year of life, it may be that a more detailed map of visual-tactile spatial correspondences enables them to coordinate visual orienting responses to tactile events, which are accurate enough to be picked up behaviourally.

Our findings suggest that infants by 6 months of age have been able to surmount at least some of the challenges in visual-tactile spatial integration posed by variations in body and limb posture. However, we do not conclude from this that infants are able to keep track of visual-tactile correspondences across all postures of their limbs. Previous studies show that an ability to incorporate information about posture into tactile processing develops gradually across the first year of life (Bremner et al., 2008; Rigato, Begum Ali, Van Velzen, & Bremner, 2014), continuing even into early childhood (Begum Ali, Cowie, & Bremner, 2014; Pagel, Heed, & Röder, 2009). In the present study, we presented bimodal visual-tactile

stimuli to the hands with those limbs in relatively familiar locations with respect to the visual field (i.e., in an uncrossed posture). Thus, it seems likely that infants of this age are able to represent visual-tactile co-location by relying on the usual location of tactile stimuli with respect to the visual field: a “canonical” representation of bodily crossmodal correspondences (see Begum Ali et al., 2014; Bremner & Cowie, 2013). The development of an ability to dynamically remap visual-tactile correspondences across changes in the posture of the arms has yet to be investigated in infancy or childhood. However, the above mentioned studies (Bremner et al., 2008; Rigato et al., 2014) strongly suggest that such developments will occur between 6 and 10 months of age.

Evidence for an ability to co-locate visual and tactile stimuli in this study has come from a visual preference for spatially incongruent trials. A preference for either congruent or incongruent trials would indicate an ability to reliably differentiate co-located and non-co-located multisensory events. Nonetheless, the direction of visual preference bears consideration. Firstly, it is notable that the observed preference for spatial incongruity in six- and ten-month-old infants is broadly consistent with a number of accounts of multisensory development. Bahrick & Lickliter’s (2012) intersensory redundancy hypothesis predicts greater preference for spatially congruent displays in young infants, but allows for attention to move more towards incongruent (or non-redundant) multisensory stimuli after the first half year of age. Gergely & Watson’s (1999) account of early social-emotional development rests on the idea of a “contingency detection module” which switches from a preference for perfect contingency (which includes spatial congruency; see also Rochat, 1998) up until 3 months of age, to a preference for imperfect contingency (including spatial incongruency) beyond that point.

Despite the agreement of our findings with the accounts discussed above, we prefer a somewhat simpler account of the visual preferences exhibited by the 6- and 10-month-olds in our study. We interpret both groups' preference for the incongruent trials as a novelty preference for a state of affairs which is not typically experienced in everyday life. It is likely that in the infant's natural environment, tactile sensations on the hands will usually be accompanied by a visual event, whether that be part of either an external cause of the bimodal visual-tactile stimulus (e.g., as in the case of a parent's hand stroking the infant's hand), or an internal cause (e.g., as in the case of the infant's hand moving to touch an object of interest). Tactile sensations are typically accompanied by visual events. This "novelty preference" interpretation is consistent with studies demonstrating that the adult perceptual system expects bimodal events to originate from a single place in external space; for instance, studies showing that the ways in which adults bind synchronously presented information across modalities (including vision and touch) often result in the perception of those events at a common location, even when that is not the case (e.g., Pavani, Spence, & Driver, 2000; Shore, Barnes, & Spence, 2006). If, as we are proposing, the preference for visual-tactile spatial incongruity does represent a novelty preference, this raises the possibility that an ability to process visual-tactile co-location is available even earlier in development. We thus anticipate that future studies to examine such abilities in younger infants would represent a fruitful line of investigation.

Some questions remain about the nature of the perceptual experiences which drove the behaviours observed in this study. For instance, it is unclear whether the infants bound the separate visual and tactile stimuli into a single perceptual event. In adults, temporally synchronous and spatially co-located stimuli have been shown to result in the perception of a multisensory event with a single origin (e.g., Körding, Beierholm, Ma, Quartz, Tenenbaum,

& Shams, 2007). Our data does not speak to the question of whether infants integrated the visual-tactile stimulation in this task as a single event. However, we can speculate about a range of possibilities. Firstly, it might be that discrimination of congruent and incongruent trials was based on a perception of a tactile and a visual stimulus (i.e. two unisensory stimuli) which were co-located in one condition but not the other. Alternatively, it is possible that the infants perceived a single bound multisensory event on congruent trials, but on congruent trials they may have perceived two unbound unisensory events or a single bound but more widespread stimulus. Importantly for the aims of the current paper, all of these possibilities necessitate an appreciation of the spatial relations between tactile and visual stimuli at some level of multisensory processing. However, it will be an important question for further research to investigate how spatial co-location is used as a cue for binding unisensory stimuli into multisensory events across early development. Research across a range of multisensory situations has suggested that such binding may not develop until 8 months of age (Neil, Chee-Ruiter, Scheier, Lewkowicz, & Shimojo, 2006), or even later (Barutchu, Crewther, & Crewther, 2009; Nardini, Jones, Bedford, & Braddick, 2008; Nardini, Begus, & Mareschal, 2013; Gori, Del Viva, Sandini, & Burr, 2008).

By investigating visual-tactile spatial links in 6- and 10-month-old infants, the present study reveals that the foundations of the multisensory abilities which underpin our perceptions of the interface between bodily and external space (Bremner et al., 2008; Eilan, 1993) are laid down within the first half year of life. Although we have demonstrated an ability to process visual-tactile spatial co-location within a single (external) spatial frame of reference in 6-month-old infants, it remains to be determined when infants first come to be able to do this. The methods used in the current report provide promising means for the study of visual-tactile spatial links in infants under 6 months of age, and offer a basis for

investigating crucial questions concerning the precise nature of multisensory representations as they emerge in early life.

REFERENCES

- Abravanel, E. (1981). Integrating the information from eyes and hands: A developmental account. In R. D. Walk & H. L. Pick, Jr. (Eds.), *Intersensory perception and sensory integration* (pp. 71-108). New York: Plenum.
- Aronson, E., & Rosenbloom, S. (1971). Space perception in early infancy: Perception with a common auditory-visual space. *Science*, **172**, 1161-1163.
- Azañón, E., & Soto-Faraco, S. (2008). Changing reference frames during the encoding of tactile events. *Current Biology*, **18**, 1044-1049.
- Bahrick, L. E. (1992). Infants' perceptual differentiation of amodal and modality-specific audio-visual relations. *Journal of Experimental Child Psychology*, **53**, 180-199.
- Bahrick, L. E., & Lickliter, R. (2000). Intersensory redundancy guides attentional selectivity and perceptual learning in infancy. *Developmental Psychology*, **36**, 190-201.
- Bahrick, L. E., Flom, R. & Lickliter, R. (2002). Intersensory redundancy facilitates discrimination of tempo in 3-month-old infants. *Developmental Psychobiology*, **4**, 352-363.
- Bahrick, L. E., & Lickliter, R. (2012). The role of intersensory redundancy in early perceptual, cognitive, and social development. In A. Bremner, D. J. Lewkowicz, & C. Spence (Eds.), *Multisensory development* (pp. 183-205). Oxford: Oxford University Press.
- Barutchu, A., Crewther, D. P. & Crewther, S. G. (2009). The race that precedes coactivation: development of multisensory facilitation in children. *Developmental Science*, **12**, 464-473.

- Begum Ali, J., Cowie, D., & Bremner, A. J. (2014). Effects of posture on tactile localization by 4 years of age are modulated by sight of the hands: evidence for an early acquired external spatial frame of reference for touch. *Developmental Science*, **17**, 935-943.
- Bremner, A. J., & Cowie, D. (2013). Developmental origins of the hand in the mind, and the role of the hands in the development of the mind. In. Z. Radman (Ed.), *The hand: An organ of the mind. What the manual tells the mental* (pp. 27-55). Cambridge, MA: MIT Press.
- Bremner, A. J., Mareschal, D., Lloyd-Fox, S., & Spence, C. (2008). Spatial localization of touch in the first year of life: early influence of a visual spatial code and the development of remapping across changes in limb position. *Journal of Experimental Psychology: General*, **137**, 149-162.
- Bryant, P. E., Jones, P., Claxton, V., & Perkins, G. M. (1972). Recognition of shapes across modalities by infants. *Nature*, **240**, 303-304.
- Butterworth, G., & Castillo, M. (1976). Coordination of auditory and visual space in newborn human infants. *Perception*, **5**, 155-160.
- Clifton, R. K., Morrongiello, B. A., Kulig, J., & Dowd, J. (1981). Newborns' orientation toward sound: Possible implications for cortical development. *Child Development*, **52**, 833-838.
- Eilan, N. (1993). Molyneux's question and the idea of an external world. In N. Eilan, R. McCarthy, & B. Brewer (Eds.), *Spatial representations: Problems in philosophy and psychology* (pp. 236-256), Oxford, UK: Oxford University Press.
- Fényes, I., Gergely, C., & Tóth, S. (1960). Clinical and electromyographic studies of "spinal reflexes" in premature and full-term infants. *Journal of Neurology, Neurosurgery & Psychiatry*, **23**, 63-68.

- Filippetti, M. L., Johnson, M. H., Lloyd-Fox, S., Dragovic, D., & Farroni, T. (2013). Body perception in newborns. *Current Biology*, **23**, 2413-2416.
- Gibson, E. J. (1969). *Principles of perceptual learning and development*. New York: Appleton-Century-Crofts.
- Gori, M., Del Viva, M., Sandini, G. & Burr D.C. (2008). Young children do not integrate visual and haptic information. *Current Biology*, **18**, 694-698.
- Graziano, M. S. A., Gross, C. G., Taylor, C. S. R., & Moore, T. (2004). A system of multimodal areas in the primate brain. In C. Spence & J. Driver (Eds.), *Crossmodal space and crossmodal attention* (pp. 51-67). Oxford, UK: Oxford University Press.
- Jaime, M., Bahrick, L., & Lickliter, R. (2010). The critical role of temporal synchrony in the salience of intersensory redundancy during prenatal development. *Infancy*, **15**, 61-82.
- Körding, K. P., Beierholm, U., Ma, W. J., Quartz, S., Tenenbaum, J. B., & Shams, L. (2007). Causal inference in multisensory perception. *PLoS ONE*, **2**, e943.
- Lampl, M., Veldhuis, J. D., & Johnson, M. L. (1992). Saltation and stasis: a model of human growth. *Science*, **258**(5083), 801-803.
- Lewkowicz, D. J. (1996). Perception of auditory-visual temporal synchrony in human infants. *Journal of Experimental Psychology: Human Perception & Performance*, **22**, 1094-1106.
- Lewkowicz, D. J. (2000). The development of intersensory temporal perception: an epigenetic systems/limitations view. *Psychological Bulletin*, **126**, 281-308.
- Lewkowicz, D. J., & Kraebel, K. S. (2004). The value of multisensory redundancy in the development of intersensory perception. In G. A. Calvert, C. Spence, & B. E. Stein

- (Eds.), *The handbook of multisensory processes* (pp. 655-678). Cambridge, MA: MIT Press.
- Lewkowicz, D. J., Leo, I., & Simion, F. (2010). Intersensory perception at birth: newborns match nonhuman primate faces and voices. *Infancy*, **15**, 46-60.
- Lewkowicz, D. J., & Turkewitz, G. (1980). Cross-modal equivalence in early infancy: Auditory-visual intensity matching. *Developmental Psychology*, **16**, 597-607.
- Lloyd, D. M., Shore, D. I., Spence, C., & Calvert, G. A. (2003). Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience*, **6**, 17-18.
- McGurk, H., & Lewis, M. (1974). Space perception in early infancy: Perception within a common auditory-visual space?. *Science*, **186**(4164), 649-650.
- Meltzoff, A. N. (1993). Molyneux's babies: Cross-modal perception, imitation and the mind of the preverbal infant. In N. Eilan, R. McCarthy & B. Brewer (Eds.), *Spatial representation: Problems for philosophy and psychology* (pp. xxx-xxx). Oxford, UK: Oxford University Press.
- Meredith, M. A., & Stein, B. E. (1996). Spatial determinants of multisensory integration in cat superior colliculus neurons. *Journal of Neurophysiology*, **75**, 1843-1857.
- Moreau, T., Helfgott, E., Weinstein, P., & Milner, P. (1978). Lateral differences in habituation of ipsilateral head-turning to repeated tactile stimulation in the human newborn. *Perceptual and Motor Skills*, **46**, 427-436.
- Morrongiello, B.A., Fenwick, K.D. & Chance, G. (1998). Crossmodal learning in newborn infants: Interferences about properties of auditory-visual events. *Infant Behavior & Development*, **21**, 543-554.
- Muir, D. W., & Field, J. (1979). Newborn infants orient to sounds. *Child Development*, **50**,

431-436.

Nardini, M., Begus, K., & Mareschal, D. (2013). Multisensory uncertainty reduction for hand localization in children and adults. *Journal of Experimental Psychology: Human Perception & Performance*, **39**, 773-787.

Nardini, M., Jones, P., Bedford, R. & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology*, **18**, 689-693.

Neil, P. A., Chee-Ruiter, C., Scheier, C., Lewkowicz, D.J. & Shimojo, S. (2006). Development of multisensory spatial integration and perception in humans. *Developmental Science*, **9**, 454-464.

Pagel, B., Heed, T., & Röder, B. (2009). Change of reference frame for tactile localization during child development. *Developmental Science*, **12**, 929-937.

Pavani, F., Spence, C., & Driver, J. (2000). Visual capture of touch: Out-of-the-body experiences with rubber gloves. *Psychological Science*, **11**, 353-359.

Pöppel, E. (1973). Comments on “Visual system’s view of acoustic space”. *Nature*, **243**, 231.

Rigato, S., Begum Ali, J., van Velzen, J., & Bremner, A. J. (2014). The neural basis of somatosensory remapping develops in human infancy. *Current Biology*, **24**, 1222-1226.

Rigato, S., Bremner, A. J., Mason, L., Pickering, A., Davis, R., & Velzen, J. (2013). The electrophysiological time course of somatosensory spatial remapping: Vision of the hands modulates effects of posture on somatosensory evoked potentials. *European Journal of Neuroscience*, **38**, 2884-2892.

Sann, C., & Streri, A. (2007). Perception of object shape and texture in human newborns: Evidence from cross-modal transfer tasks. *Developmental Science*, **10**, 399-410.

- Sherrington, C. S. (1910). Flexion-reflex of the limb, crossed extension-reflex, and reflex stepping and standing. *Journal of Physiology*, **40**, 28-121.
- Shore, D. I., Barnes, M. E., & Spence, C. (2006). Temporal aspects of the visuotactile congruency effect. *Neuroscience Letters*, **392**, 96-100.
- Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, **9**, 255-266.
- Spelke, E. (1976). Infants' intermodal perception of events. *Cognitive Psychology*, **8**, 553-560.
- Streri, A. (2012). Crossmodal interactions in the human newborn: new answers to Molyneux's question. In A. J. Bremner, D. J. Lewkowicz, & C. Spence (Eds.), *Multisensory development* (pp. 88-112). Oxford, UK: Oxford University Press.
- Streri, A., & Gentaz, E. (2003). Cross-modal recognition of shape from hand to eyes in human newborns. *Somatosensory & Motor Research*, **20**, 13-18.
- Streri, A., & Gentaz, E. (2004). Cross-modal recognition of shape from hand to eyes and handedness in human newborns. *Neuropsychologia*, **42**, 1365-1369.
- Van Hof, P., van der Kamp, J., & Savelsbergh, G. J. P. (2002). The relation of unimanual and bimanual reaching to crossing the midline. *Child Development*, **73**, 1353-1362.
- Walker-Andrews, A. (1994). Taxonomy for intermodal relations. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 39-56). Hillsdale, NJ: Lawrence Erlbaum.
- Wallace, M. T., Roberson, G. E., Hairston, W. D., Stein, B. E., Vaughan, J. W., & Schirillo, J. A. (2004). Unifying multisensory signals across time and space. *Experimental Brain Research*, **158**, 252-258.
- Wertheimer, M. (1961). Psychomotor coordination of auditory and visual space at birth.

Science, **134**, 1692.

Zappella, M., & Simopoulos, A. (1966). The crossed-extension reflex in the newborn.

Annales Paediatricae Fenniae, **12**, 30-33.

FIGURE CAPTIONS

Figure 1: A schematic illustration of the stimulus presentation protocols used in the reported experiment (both age groups). Panel A shows the spatially congruent visual-tactile event sequences, and Panel B shows the incongruent sequences. In Panel A co-located bimodal (visual-tactile) stimulation (700 ms) is presented synchronously on a single hand at a time, alternating between left and right hand. In Panel B the visual and tactile stimuli alternate between the hands according to the same schedule, but although they are presented synchronously they never coincide on the same hand. Panel C displays a schematic of the stimulus presentation schedule within a single trial.

Figure 2: The mean duration of infants' looking at their hands during congruent and incongruent test conditions (in seconds), plotted according to age group. Error bars represent the standard error of the mean.

Figure 1

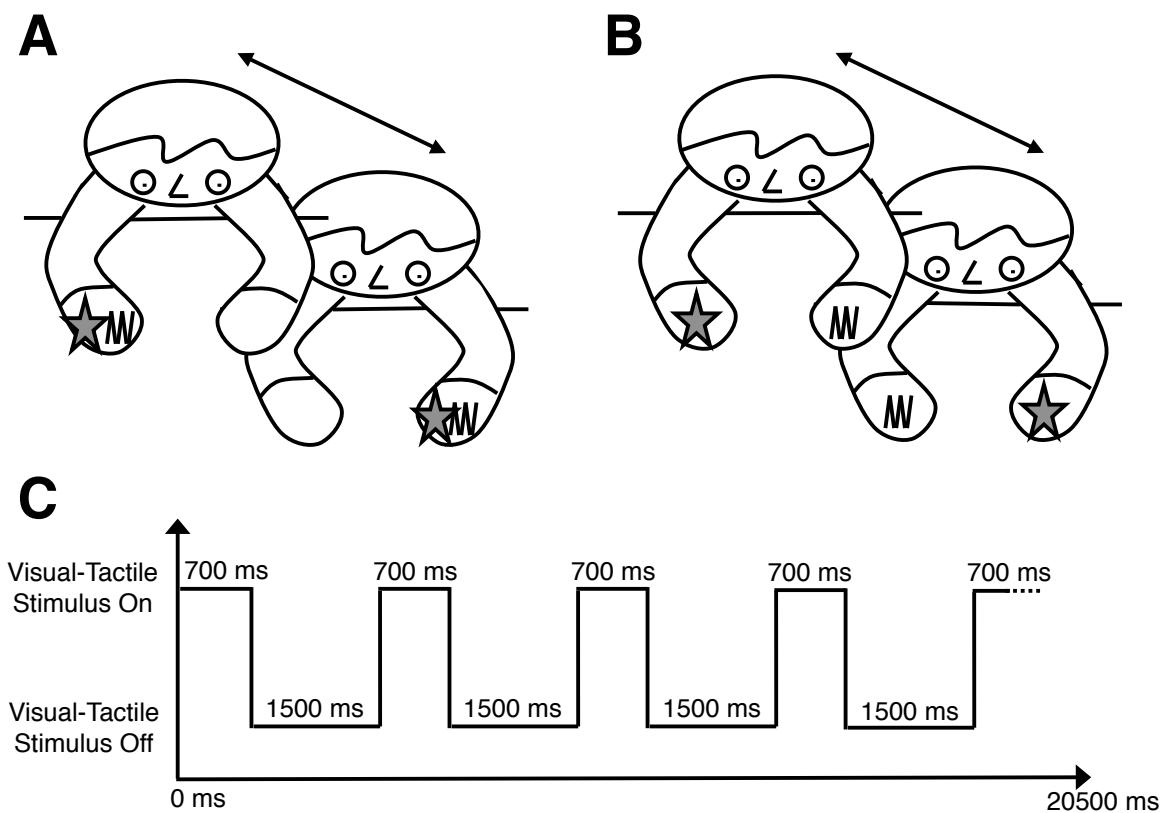


Figure 2

