

1 Opinion

2 **Infants lost in (peripersonal) space?**

3

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16

**Abstract**

17

18           A significant challenge in developing spatial representations for the control of  
19 action is one of multisensory integration. Specifically we require an ability to  
20 efficiently integrate sensory information arriving from multiple modalities pertaining  
21 to the relationships between the acting limbs and the nearby external world (i.e.,  
22 peripersonal space), across changes in body posture and limb position. Evidence  
23 concerning the early development of such spatial representations points towards the  
24 independent emergence of two distinct mechanisms of multisensory integration. The  
25 earlier-developing mechanism achieves spatial correspondence by representing body  
26 parts in their typical or default locations, and the later-developing mechanism by  
27 dynamically remapping the representation of the position of the limbs with respect to  
28 external space, following changes in postural information arriving from  
29 proprioception and vision.

30

### 31 **Embodied spatial representations**

32 When we explore extrapersonal space, not only do we register its objective  
33 properties, but we also perceive its affordances for action and interaction [1]. In order  
34 to act on our environment, we require “embodied” representations of the locations of  
35 objects coded with respect to our body and limbs. Numerous advances in our  
36 understanding of embodied processes in mature adults and non-human animals have  
37 emerged in recent years. Notably, neuroscientific research has uncovered evidence for  
38 the existence of neural circuits that selectively represent the multisensory space within  
39 immediate reach; “peripersonal space” [2-8]. The distinction between peripersonal  
40 space and extrapersonal space has, however, remained largely unexplored by  
41 developmental researchers (e.g., [9,10]). In this paper, we show how seemingly  
42 conflicting findings from research on early spatial abilities in infancy can be resolved  
43 by considering spatial representations in an embodied context. We outline some of the  
44 specific computational challenges associated with peripersonal representations and,  
45 based on recent behavioural and neuroscientific research, propose a two-mechanism  
46 framework for explaining the development of spatial representations underlying  
47 action in peripersonal space.

48

### 49 **Conflicting findings in research on infants’ spatial development**

50 Before infants begin to manipulate objects and navigate through their  
51 environments, they have little obvious need for detailed spatial representations. Yet  
52 research using measures of looking duration has shown that, within a few months of  
53 birth, human infants are able to form sophisticated spatial representations of their  
54 environment [11,12]. For instance, by 3-4 months of age infants form the perceptual  
55 categories of “above” and “below” [13], and encode the spatial distance between

56 objects [14]. Strikingly, young infants can also recognise the locations of objects and  
57 features in relation to external frames of reference across changes in their orientation  
58 [15-17].

59 However, while looking-duration measures of “spatial recognition” ([14-17];  
60 see Box 1) have tended to indicate precocious abilities to represent stimulus locations  
61 relative to external frames of reference, “spatial orienting” tasks have provided a  
62 mixed picture of early spatial abilities. When orienting to targets, young infants seem  
63 to code their responses with respect to their own body and ignore changes in the  
64 target’s or their own position. When either is moved before the orienting response  
65 occurs, young infants make ‘egocentric’ errors, and it is only in their second year that  
66 they correctly update their responses ([18,19]; Box 1 compares spatial recognition and  
67 orienting tasks).

68 --Insert Box 1 about here--

69 One way of resolving these conflicting findings is to consider the kinds of  
70 spatial reference required in these two different types of task. In recognition tasks, it is  
71 possible to identify changes in the location of objects by reference to environmental  
72 features. By contrast, orienting tasks require infants both to represent the location of  
73 objects with respect to their own body (in order to direct their orienting responses),  
74 *and* to update this body-centered location in response to any changes in their  
75 orientation with respect to the environment. Thus, infants’ poorer performance in  
76 spatial orienting tasks may reflect their difficulties with registering correspondences  
77 between the location of targets in the environment, and the intrinsic body-centered  
78 coordinates required to orient to them. Such difficulties may help explain a well-  
79 known paradox of cognitive development in the first year of life: that infants’ early  
80 competence at representing spatiotemporal information about objects, as

81 demonstrated in looking-duration measures (e.g., [11]), is not matched by their ability  
82 to act manually on that information until much later in their first year (see [24-28]).

83         Regardless of discussions concerning early knowledge about objects and  
84 space, the relatively protracted development of spatial orienting abilities in infancy  
85 brings into focus the need for further research into the early development of spatial  
86 representations for action. We know relatively little about the developmental  
87 emergence of representations of the relationship between the environment and the  
88 spatial coordinates for action within that environment - that is, the development of  
89 *peripersonal spatial* representations.

90

#### 91         **Forming representations of peripersonal space: The postural challenge**

92         Despite the limited consideration given to the development of peripersonal  
93 spatial abilities (e.g., by Piaget [20]), locating objects in peripersonal space is a non-  
94 trivial problem. For, in order to retrieve an object, one's brain must represent the  
95 object's location via the distal spatial senses (i.e., vision and audition), and also take  
96 into account the location of the retrieving limb relative to the object. The necessary  
97 multisensory information specifying the layout of our body with respect to the world  
98 is typically provided by touch, proprioception, vision, and occasionally audition. A  
99 major difficulty arises at this point, because the limbs and body move relative to each  
100 other and to visual and auditory space whenever posture changes. The challenge  
101 posed by this postural variation is even more complex when considered across  
102 development, as not only do the relative sizes and shapes of the limbs, body, and head  
103 change rapidly from month to month [29], but, the number and variety of postural  
104 changes which an infant can readily make also increase with age [30-34].



130 information. But it can also lead to errors (as highlighted by striking bodily illusions,  
131 such as the “rubber hand” and “mirror” illusions [48-50]). The greater weighting of a  
132 visual frame of reference can also be observed in the absence of direct visual spatial  
133 cues. When adults make temporal order judgments (TOJs) concerning tactile stimuli  
134 presented on one hand then the other in quick succession, performance is much less  
135 accurate in the unusual crossed-hands posture, than in the more typical uncrossed-  
136 hands posture. Thus, representations of stimuli in peripersonal space can rely on a  
137 spatial frame of reference defined by the usual layout of the body with respect to  
138 vision [51-54].

139 ii) *Postural remapping*: By taking account of postural changes (either  
140 passively, through visual and proprioceptive cues, or actively, through “efferent  
141 copies” of the movement plans used to change posture), the spatial correspondence  
142 between distal targets and the limbs can be “re-mapped”. The research described in  
143 Box 2 points to the existence of such an integrative mechanism in human and non-  
144 human primates. The action of this mechanism can also be observed in adults’  
145 saccades to tactile stimuli. If saccadic orienting responses to tactile stimuli are  
146 delayed by 600-1000ms, then they are directed appropriately in visual space, even  
147 when the touch is delivered in an unfamiliar or atypical location (such as in the  
148 opposite visual hemifield when the hands are crossed [55]; see Figure 1). Thus, it  
149 seems that an integrative mechanism that is sensitive to posture is required in order to  
150 make correct gaze-orienting responses to atypical hand locations.

151 --Insert Figure 1 about here--

152 Bremner et al. [56] recently examined the development of these mechanisms  
153 of multisensory integration in 6.5- and 10-month-old infants, by measuring their  
154 spontaneous manual orienting responses to vibrotactile sensations presented to the

155 infants' hands in uncrossed-, and crossed-hands postures (see Figure 2a). The 6.5-  
156 month-olds demonstrated a bias to respond in the direction appropriate to the  
157 uncrossed-hands posture across both arm postures thus indicating a reliance on the  
158 typical location of the tactile stimulus in visual space. Later, at 10 months, manual  
159 responses were made appropriately in both postures, suggesting the development of  
160 an ability to take account of posture in remapping correspondences between visual  
161 and tactile stimulation.

162 --Insert Figure 2 about here--

163 These developmental findings converge with neuroscientific and behavioural  
164 research in suggesting that representations of peripersonal space arise from two  
165 distinct mechanisms of sensory integration, which follow separate developmental  
166 trajectories. The first mechanism, *visual spatial reliance*, integrates bodily and visual  
167 sensory information but relies substantially on the probable location of the hand,  
168 derived primarily from visual information and prior experience. This mechanism is  
169 present early in the first 6 months of life. The second mechanism, *postural*  
170 *remapping*, updates these multisensory spatial correspondences by dynamically  
171 incorporating information about the current hand and body posture. This mechanism  
172 develops after 6.5-months of age. We are not suggesting that the early mechanism of  
173 *visual spatial reliance* is wholly replaced by that of *postural remapping* but that they  
174 continue to work together as is observed in adults [37-39,51-55] (see Figure 2b).

175 Of the measurable behaviours in early infancy, perhaps the most relevant ways  
176 to observe the development of such mechanisms of peripersonal space are reaches and  
177 grasps made towards nearby objects in nearby space.

178 --Insert Box 3 about here--

179



**180 Spatial representations guiding early reaching**

181 Box 3 summarises some of the major developments in reaching observed in  
182 the first year. A key question raised by the framework outlined here concerns whether  
183 infants' reaches at any given stage of development are based on neural systems that  
184 take account of current limb posture ("postural remapping"), or whether instead  
185 successful reaches are based on prototypical representations of the limbs in their  
186 familiar locations derived from visual experience ("visual spatial reliance") [67].  
187 Given that infants' first successful reaches towards visual targets can occur without  
188 any visual input concerning the position of their limbs it seems that these actions are  
189 generated within multisensory peripersonal spatial representation. Nonetheless it  
190 remains possible that their reaches in the dark are not guided by current  
191 proprioceptive information, but rather by a multisensory representation of limb  
192 position that is strongly weighted towards the location that the limb would normally  
193 occupy in the visual field. Because studies of infants' reaching in the dark [60-62]  
194 have not systematically varied limb posture prior to reaching, it is difficult to  
195 disentangle these interpretations (cf. [49]). However, within the novel framework put  
196 forward here, the predictions are that if posture were to be varied, young infants' early  
197 reaches would be error-prone, but that in the second 6 months they will become better  
198 able to take account of the current position of the limbs in order to reach accurately  
199 from a variety of starting postures.

200 Improvements in the ability to use postural information to maintain spatial  
201 alignment between different sensory inputs arising from peripersonal space can also  
202 explain the later development of infants' ability to produce more fine-grained ("goal-  
203 directed") postural adjustments (especially those made without sight of the hand [65];

204 see Box 3). These behaviors clearly require postural calibration, and feed-forward  
205 prediction in actions made towards objects.

206

### 207 **Neural construction of peripersonal space**

208 We have argued that two mechanisms of multisensory integration underlying  
209 peripersonal space (“visual spatial reliance” and “postural remapping”) develop  
210 independently in the first year of life. The sensory interactions subserving the early  
211 “visual spatial reliance” mechanism could be governed both by subcortical (e.g., the  
212 superior colliculus (SC) or putamen) and cortical loci for multisensory integration  
213 (see Box 2). The strongest evidence for neural systems underlying the dynamic  
214 updating of peripersonal space across changes in posture (“postural remapping”) has  
215 been obtained from single unit recordings made in macaque premotor cortex [42,43].  
216 Thus, the more protracted development of mechanisms subserving postural remapping  
217 could be explained by a developmental shift from sub-cortical to cortical processing  
218 of multisensory stimuli in early infancy [68]. However, a number of factors speak  
219 against cortical maturation as the sole explanation for these developments.

220 Firstly, there have been a number of demonstrations of the effect of experience  
221 on multisensory integration. In one study [69], a newborn chimpanzee’s multisensory  
222 and motor experience with his own hands and feet was severely restricted during the  
223 first 30 months of life by fixing restricting cylinders over these limbs. This  
224 chimpanzee later demonstrated almost no ability to learn a conditioned crossmodal  
225 orienting response between two tactile cued locations on the index finger of either  
226 hand. Consistent with this finding, neurophysiological evidence has demonstrated that  
227 multisensory neurons in the SC of dark-reared cats fail to demonstrate the normal  
228 distinct responses to multisensory and unimodal stimuli [70].

229 More recently, Röder et al. [71] have shown that early visual experience may  
230 play a key role in establishing how tactile stimuli are related to visual spatial  
231 coordinates, and the typical (visual) posture of the limbs. Using the tactile TOJ task  
232 described earlier [51-54], they found that, unlike normally sighted or blindfolded  
233 adults, congenitally blind participants exhibited no impairment in the crossed-hands  
234 posture. Late blind participants showed similar crossed-hands impairments to those of  
235 the sighted participants, indicating that early visual experience is necessary for the  
236 normal development of tactile spatiotemporal perception [72]. Indeed, there are a  
237 number of indications that changes in patterns of sensory weighting in spatial tasks  
238 may continue well beyond infancy and into late childhood [73-77].

239 Secondly, the more protracted development of postural remapping in infancy  
240 may depend largely on changes in the kinds of *active* experience that infants have of  
241 their environment. Indeed, the developments in postural remapping observed between  
242 6.5 and 10 months coincide with the emergence (at about 6 months) of spontaneous  
243 reaching towards and across the midline for visually-presented objects [32-34]. The  
244 multisensory experience associated with this behaviour is well-suited for driving the  
245 development of postural remapping mechanisms.

246 Roles for experience in the development of representations of peripersonal  
247 space are consistent with “interactive specialization” frameworks for neural systems  
248 development [23,78] in that some degree of specialization of earlier developed brain  
249 regions (such as the SC) for multisensory orienting responses may lay down the  
250 behavioural foundations required for experientially-driven development of more  
251 specialized networks underlying peripersonal representations. The provision of a  
252 default prototypical representation of peripersonal space underpinned by patterns of  
253 relative weighting of the senses may provide a basis upon which (later developing)

254 experience-dependent dynamic networks can be efficiently deployed, when changes  
255 in the posture of the body make this necessary for successful orienting. This is not to  
256 say that brain networks underlying a default prototypical representation would be  
257 unaffected by experience. Changes in the body across development would require  
258 such networks to be flexible, and indeed evidence suggests that sensory experience is  
259 necessary for their normal development (cf. [71]). Rather, it seems more reasonable to  
260 suggest that the general function of such networks in establishing a unitary (if vague)  
261 default representation of peripersonal space may be well specified prior to birth.

262

### 263 **Conclusions**

264 A significant challenge to infants in the first year of life is in forming detailed  
265 accurate representations of multisensory peripersonal space. Indeed the challenges  
266 posed by this problem may help explain some of the puzzling dissociations between  
267 perception and action uncovered in studies of early cognitive development [24-28].  
268 The framework presented here argues for the independent development (at least over  
269 the first year of life) of two integrative mechanisms that give rise to multisensory  
270 representations of peripersonal space: *Visual spatial reliance* and *postural remapping*.  
271 We have argued that a mechanism of visual spatial reliance provides a rough default  
272 multisensory integration, upon which more dynamic systems of integration can later  
273 be efficiently deployed. The later development of more dynamic integrative systems  
274 may arise in response to changes in the demands of multisensory and sensorimotor  
275 interactions in peripersonal space, commensurate with the emergence of certain kinds  
276 of postural changes related to exploratory behaviours. Future data notwithstanding,  
277 we present this as a framework for considering the early development of

278 representations of the space in which we act. Several future research questions (see  
279 Box 4) will help enlighten this vital area of study.

280 --Insert Box 4 about here--

281

282

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285

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464 Box 1: Paradigms for investigating spatial representation in infants

465 Methods for examining infants' spatial representations can be classified into  
466 spatial "recognition", and "orienting" tasks. Spatial recognition tasks [14-17] (Box 1  
467 Figure ia) take advantage of infants' tendency to look preferentially towards novel or  
468 familiar spatial arrays. The infant is first habituated to a particular spatial array. To  
469 examine in which reference frame habituation occurred, the infant or the array is  
470 moved and the infant's preferential looking behaviour is observed. By contrast, spatial  
471 orienting tasks [18,19] (Box 1 Figure ib) make use of infants' directional (visual or  
472 manual) responses to a given location. In these tasks, infants' are led to expect a  
473 stimulus at a particular location. Again, to determine which frame of reference they  
474 use, either the array or the infant is moved before the directional response is made (in  
475 anticipation of an event, or in the context of goal-directed reaching).

476 --Insert Box 1 Fig i about here--

477 The precocious spatial abilities demonstrated in spatial recognition studies  
478 measuring looking duration contrast with the limited abilities demonstrated in spatial  
479 orienting tasks [18-23], which have tended to support Piaget's [20] account of spatial  
480 development in infants. Piaget argued that infants are initially reliant on an egocentric  
481 (body-centered) spatial code and only later construct objective representations of  
482 external space through patterns of activity in their environment.

483 While the representation of objects within external frames of reference by  
484 young infants (as revealed by "spatial recognition" tasks) is inconsistent with Piaget's  
485 [20] framework, the necessity of explaining the delayed development of spatial  
486 orienting abilities suggests another possible, constructionist, account: That is,  
487 development may proceed via the construction of spatial representations of the  
488 relationships between the location of targets and the sensorimotor coordinate

489 transformations required to perform actions upon those targets – the development of

490 peripersonal spatial representations.

491



492 Box 2: Neural and behavioral correlates of peripersonal spatial representations

493 Peripersonal representations require multisensory integration between the  
494 body senses (somatosensation, proprioception, and kinaesthesia) and the distal senses  
495 (vision and audition). The superior colliculus (SC) has long been identified as a brain  
496 region in which neurons respond to multisensory stimuli in approximate spatial  
497 register [35,36]. Multisensory neurons in the SC code stimuli in terms of the motor  
498 responses required to orient the eyes and head to the location of those stimuli (i.e., in  
499 a multisensory-motor map of space). More recently, research with macaques [2,3] has  
500 revealed neurons in a region of premotor cortex (and other brain areas) which have  
501 similar multisensory properties, but which code stimulus location with respect to  
502 individual body parts such as the arm, or the mouth. Such cells likely play an  
503 important role in generating and controlling rapid multisensory-guided target-directed  
504 or avoidance movements.

505 A frequently-used manipulation when studying peripersonal space is to cross  
506 the hands over the midline (Figure 3a). This manipulation changes the spatial  
507 correspondence of body sense information to distal locations such that hemispheric  
508 correspondence between inputs from these senses is reversed [37,38]. Thus, the  
509 appropriate integration of sensory information coming from the body and the distal  
510 array, requires some form of spatial remapping.

511 Research with adult humans has shown that multisensory interactions in  
512 attentional processes take account of postural changes across the midline [39].  
513 Additionally, the same brain areas identified as sites of multisensory integration have  
514 been implicated in processes of postural remapping. Neurons that remap sensory  
515 correspondences across changes in posture have been reported in the monkey SC  
516 [40,41] and premotor cortex [42,43].

517

518 Box 3: The development of reaching behaviour in the first year of life

519 While newborn infants do not often manually contact objects, their reaches are  
520 more often directed towards an object if they are looking at it [57,58]. Newborns have  
521 also been shown to change the position of their hand in order to bring it into sight  
522 under the illumination of a spotlight which alternated between two locations near their  
523 body [59]. Thus, at birth there is at least some spatial integration between the  
524 information coming from nearby visible objects, and that coming from the body parts  
525 with which responses are made.

526 A key question is whether early reaching is guided by visual feedback  
527 concerning the relative locations of hand and object. That newborns demonstrate a  
528 deceleration of their arm's movement in anticipation of their hand's appearance in the  
529 spotlight [59] is suggestive of a coordination of visual, proprioceptive, and  
530 kinaesthetic information (purely visual guidance cannot explain the anticipatory  
531 adjustments, since the hand was invisible when outside the spotlight). However, it is  
532 difficult to determine whether this indicates early crossmodal spatial correspondence  
533 between proprioceptive and visual space, or rather operant conditioning of particular  
534 arm movements, contingent upon the reward of seeing one's hand.

535 The coordination of proprioceptive and visual space in the guidance of  
536 reaching has been investigated more fully by comparing infants' early successful  
537 reaches for distal targets in the light against those in the dark (i.e., towards sounding  
538 or glowing targets without visual cues to the location of their hand) [60-62]. These  
539 studies have shown that successful reaching in the dark develops at the same age as in  
540 the light, indicating that the first reaches (at around 3-4 months of age) can be based  
541 on proprioceptive guidance of hand position towards a sighted visual target. However,  
542 an as yet unaddressed question concerns whether this proprioceptive guidance

543 constitutes a representation of the current posture of the body, or one which defines  
544 the location of the limbs with respect to their typical location in visual space (see  
545 main text).

546         From four months of age, reaches gradually become more “goal-directed” in  
547 nature. Grasps which anticipate the orientation of an object begin to emerge at around  
548 five months [63,64]. By 8 months, re-orienting of the hand in anticipation of the  
549 orientation of a visual target also occurs independently of vision of the hand [65],  
550 indicating that postural guidance is achieved proprioceptively at this age. Grasps  
551 which anticipate the size of an object are first observed from nine months of age [66].  
552

553

Box 4: Questions for future research

- 554 • How is the emergence of peripersonal spatial abilities related to developing brain  
555 function?
- 556 • Neurons have been found in parietal and premotor areas which, when stimulated,  
557 trigger defensive reactions to stimuli approaching the body [2,3]. Can the ability  
558 to make accurate defensive reactions to such stimuli be traced in infancy?
- 559 • Which experiences drive the development of postural remapping in infants? What  
560 role do exploratory manual behaviours play in this development? Longitudinal  
561 training studies may be used to investigate these questions.
- 562 • In adults, patterns of visual-proprioceptive sensory weighting in manual control  
563 vary depending on the spatial dimension in which stimuli are localized (e.g.,  
564 depth vs. azimuth [47]), as predicted by the principle of optimal integration [46].  
565 Recent research has indicated that optimal integration in navigational and form  
566 discrimination tasks develops through childhood and into adolescence [76,77].  
567 But do patterns of sensory weighting in early reaching behaviours follow a  
568 similar trajectory of sub-optimal to optimal integration? Are early processes of  
569 sensory weighting in infants' reaching characterized by the dominance of one  
570 modality, as is the case with young children's form discrimination abilities [77]?
- 571 • What are the relationships between the development of representations of one's  
572 own peripersonal space, and that of others (see [79])?
- 573 • Are early abilities to recognize one's own body (see [80]), like early  
574 representations of peripersonal space, also dependent upon the prototypical layout  
575 of the limbs?

576

577

Glossary

578 **Embodied representations:** Representations of the external environment in relation  
579 to the perceiver's body (including their individual limbs). Embodied representations  
580 are required if one is to act upon the environment.

581 **Efferent copies:** Copies of motor commands sent from motor regions to other regions  
582 that are not involved in the immediate control of movement, which can be used, for  
583 example, to update representations of current limb position, thus providing a rapid  
584 estimate of current limb position, independently (or in advance of) sensory input.

585 **Extrapersonal space:** The space beyond the body (cf. personal space). Extrapersonal  
586 space can be sub-divided into that which is out of reach of the body and that which is  
587 in reach of the body (peripersonal space).

588 **Mirror Illusion:** Participants sit with both arms held out straight in front of their  
589 body, with a mirror placed between them - one arm is hidden, the other is visible  
590 directly and via reflection. The reflected arm provides a visual substitute for the  
591 hidden arm. Changing the distance of either arm from the mirror results in the  
592 'virtual' and the real arm occupying different locations. This conflict between vision  
593 and proprioception leads to a recalibration of proprioception towards vision, and the  
594 illusion that the 'virtual' arm is, in fact, the real arm.

595 **Multisensory space:** A neural representation of space that encodes stimulus location  
596 across multiple sensory modalities in a similar way – for example, in a single map of  
597 space in which individual neurons respond to visual, auditory, and somatosensory  
598 stimuli arising from approximately the same location. Such maps are found in the  
599 superior colliculus, posterior parietal cortex, and the premotor cortex.

600 **Peripersonal space:** The reachable space immediately surrounding the body and  
601 limbs or individual body parts.

602 **Rubber Hand Illusion:** A phenomenologically striking illusion in which participants  
 603 feel their own hand being stroked with a brush, while watching a dummy hand being  
 604 stroked in synchrony. Soon participants come to feel that the visible strokes are  
 605 identical to the felt strokes, that their perception of touch has been ‘captured’ by or  
 606 referred onto the dummy hand, and, that the dummy hand is, in fact, their own hand.

607 **Spatial orienting:** Moving or preparing to move an effector (e.g., a finger or hand),  
 608 or a sensory organ (e.g., the fovea) towards a specific target in space.

609 **Spatial recognition:** The recognition of a spatial relationship between a feature and a  
 610 frame of reference which can be either intrinsically defined (e.g., the body, the retina),  
 611 or extrinsically defined (e.g., in relation to the layout of a room, or in relation to an  
 612 axis of an object).

613 **Superior Colliculus (SC):** A subcortical mid-brain area which receives input from  
 614 multiple sensory modalities (vision, audition, touch etc.). The SC has been studied  
 615 extensively in cats and ferrets, and is strongly implicated in the initiation of saccadic  
 616 eye and head orienting responses.

617 **Premotor Cortex:** A large cortical territory immediately anterior to primary motor  
 618 cortex, which receives input from multiple sensory modalities and cortical areas. This  
 619 region has been studied extensively in macaque monkeys and is associated, among  
 620 other things, with the dynamic updating of limb and body position, the representation  
 621 of stimuli in the space immediately surrounding the limbs (peripersonal space), and  
 622 the selection, generation and control of bodily movements.

623 **Principle of Optimal Integration:** Information arising from different sensory  
 624 modalities, or different sources, may differ in variability from situation to situation (or  
 625 task to task). A signal arising from a source with high variability is less reliable than a  
 626 signal arising from a source with low variability. Optimal integration combines the

627 information provided by different sources in proportion to their reliability, thus

628 maximising the reliability of the combined estimate.

629

## 630 Figure Captions

631

632 Box 1 Fig. i: Paradigms for investigating spatial reference in early infancy. Figure  
633 1a: Simplified illustration of a spatial recognition paradigm [17]. In this  
634 study, 6.5-month-old infants dishabituated (demonstrated increases in  
635 looking following familiarization; indicated by alert eyes) to displays  
636 in which the object had moved, irrespective of whether they themselves  
637 had moved relative to the spatial array. That is, they used an  
638 environmental spatial reference. Figure 1b: Simplified illustration of a  
639 spatial orienting paradigm [19]. In this study, 9-month-old infants  
640 observed an object being hidden at one of two locations, and were then  
641 moved to the other side of the spatial array and allowed to search  
642 manually. The typical responses at nine months were incorrect,  
643 indicating their use of an egocentric spatial reference.

644 Figure 1: Saccades made by one adult human to tactile stimuli on their right hand  
645 in a crossed-hands posture (with the right hand in the left visual field).  
646 Panel A - saccades are made to the tactile stimulus without any  
647 intervening delay, and Panel B - saccades are made to the tactile  
648 stimulus with a delay of 600-1000 ms between stimulus and response.  
649 Gradations indicate 10 degrees of visual angle. Note that in A the  
650 majority of saccades begin by heading in the direction in which the  
651 tactile stimulus would normally lie and then a later corrective process  
652 takes account of current hand posture, and shifts the saccade direction.  
653 (Redrawn from [55]).

654 Figure 2: Integrate this! In the uncrossed-hands posture both the visual



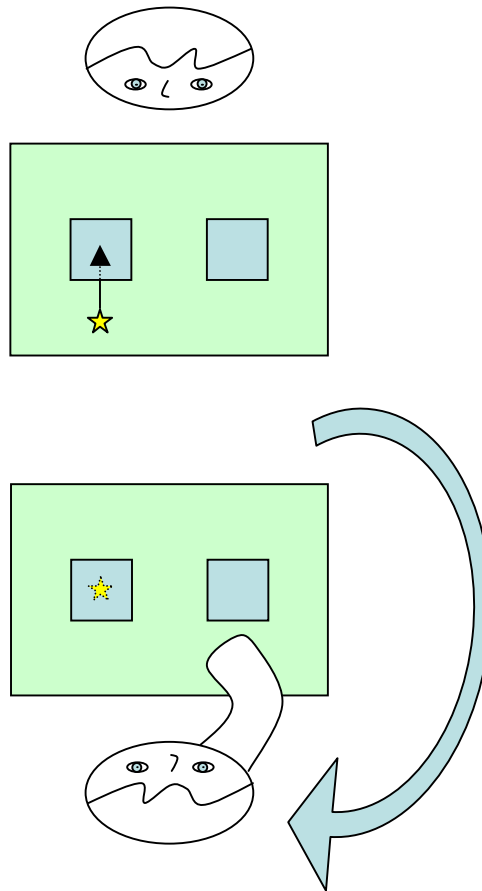
655 information about the hand (circle) and a tactile stimulus on that hand  
656 (zig-zag pattern) arrive at the contralateral hemisphere. But with  
657 crossed-hands, these signals initially arrive in opposite hemispheres  
658 (Panel A). Panel B shows the sources of information available to be  
659 integrated into a representation of stimulus location. Our framework  
660 suggests that all sources of information are available to 10-month-olds,  
661 and all but current postural information is available to 6.5-month-olds.  
662 Panels C and D show 6.5- (C) and 10-month-old (D) infants' manual  
663 responses to tactile stimuli. The infants' first responses on each trial  
664 were coded (from video-recordings) in terms of their direction in visual  
665 space with respect to the hemisphere receiving the tactile signal. Thus,  
666 contralateral responses are appropriate in the uncrossed-hands posture,  
667 and ipsilateral responses in the crossed-hands posture. The 6.5-month-  
668 olds' manual responses (Panel C) showed an overall contralateral bias,  
669 as predicted by a hypothesized reliance on the typical layout of their  
670 body relative to vision. The 10-month-olds (Panel D) were able to  
671 respond manually in the appropriate direction in either posture,  
672 suggesting, in agreement with the proposed framework, that this age-  
673 group are able to use information about current posture to remap their  
674 orienting responses (Figure adapted from [56]). Asterisks represent  
675 significant comparisons. Solid arrows represent a strong contribution of  
676 a particular source of information to behavior. Dotted arrows represent  
677 a weak contribution of the same.  
678

679

Figure 1

680

681

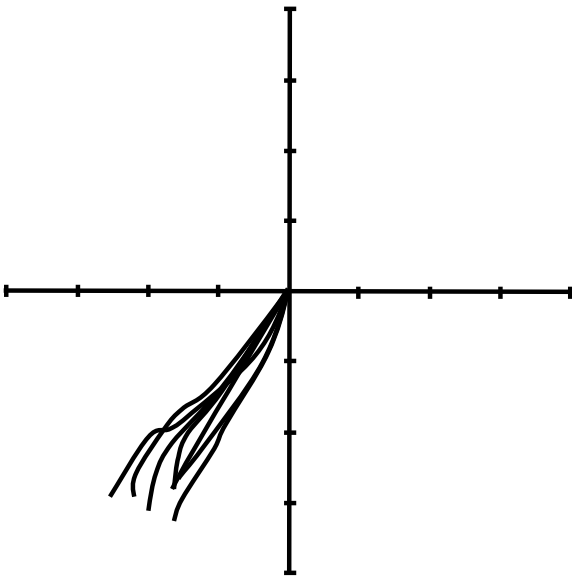
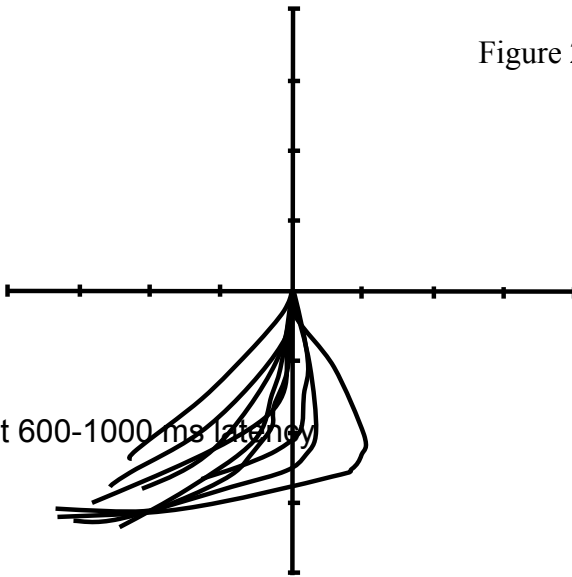


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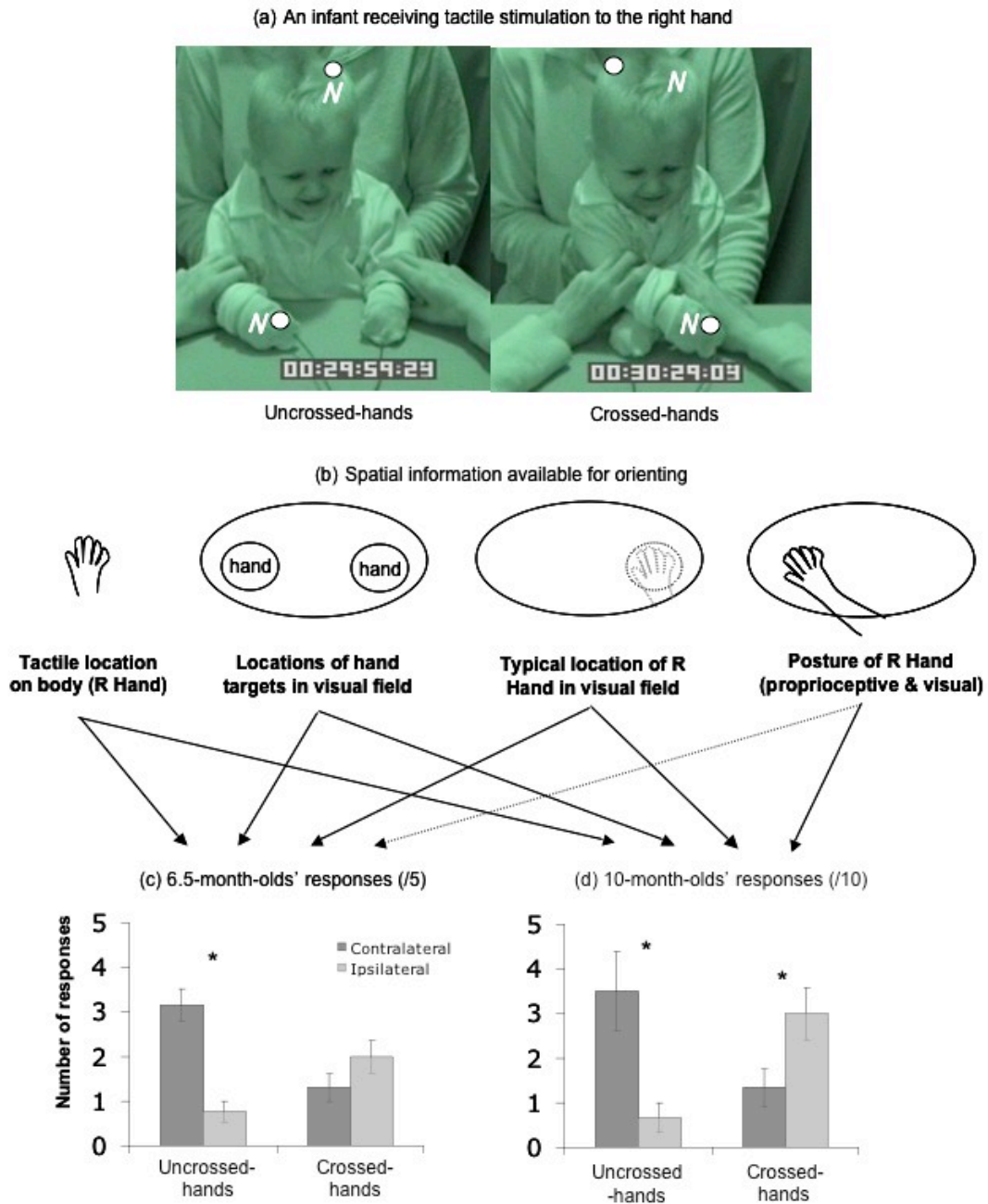
Figure 2

(b) Saccades at 600-1000 ms latency



684

Figure 3



685