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Development of space perception in relation to the maturation of the motor system in infant rhesus macaques (*Macaca mulatta*)

Valentina Sclafani [a,*], Elizabeth A. Simpson [a,b], Stephen J. Suomi [b], Pier Francesco Ferrari [a]

[a] *Dipartimento di Neuroscienze, Università di Parma, Via Volturno 39 – 43100 Parma, Italy*
[b] *Eunice Kennedy Shiver National Institute of Child Health and Human Development, Laboratory of Comparative Ethology, Poolesville, MD, USA*

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ABSTRACT

To act on the environment, organisms must perceive object locations in relation to their body. Several neuroscientific studies provide evidence of neural circuits that selectively represent space within reach (i.e., peripersonal) and space outside of reach (i.e., extrapersonal). However, the developmental emergence of these space representations remains largely unexplored. We investigated the development of space coding in infant macaques and found that they exhibit different motor strategies and hand configurations depending on the objects' size and location. Reaching-grasping improved from 2 to 4 weeks of age, suggesting a broadly defined perceptual body schema at birth, modified by the acquisition and refinement of motor skills through early sensorimotor experience, enabling the development of a mature capacity for coding space.

Introduction

A central issue in cognitive development is how the brain constructs a map of the surrounding world and how this map interacts with the internal representation of one's body. To interact with an object, it is necessary to determine whether an object is in the near-reachable space or in the far-unreachable space. The capacity to discriminate an object as reachable involves not only information about properties of objects and affordances for action and interaction, but also spatial information of objects and their relation to the body and the possibilities of acting (Witt et al., 2004).

Objects in peripersonal space, that is, the space immediately surrounding the body, can be easily grasped and manipulated, whereas objects located beyond this space (i.e., extrapersonal space) cannot be reached without moving the torso towards the object. To plan appropriate behavioral patterns, the brain needs to differentiate objects situated in peripersonal space from those in extrapersonal space (Previc, 1990, 1998; Rizzolatti et al., 1988; Rizzolatti et al., 1997). In support of this, neurophysiological experiments in adult nonhuman primates and neurologically impaired human patients reveal that the space immediately surrounding the body is represented differently than space farther away (Brain, 1941; Sommer, 1969). Furthermore, the brain has different ways of coding the position of objects placed at different locations with respect to the body (Iriki et al., 1996; Làdavas, 2002; Shelton et al., 1990).

Other neurophysiological studies in monkeys reveal additional details of how different brain areas are involved in space coding (Rizzolatti and Luppino, 2001). For example, bimodal neurons, which code for peripersonal and extrapersonal space, have been described in inferior parietal areas and the ventral premotor cortex (Duhamel et al., 1998; Fogassi et al., 1992, 1996; Graziano and Cooke, 2006; Graziano et al., 1994; Graziano and Gross, 1998). These neurons are activated by visual as well as somatosensory stimulation applied to specific body parts, and exhibit higher activity when visual stimuli are within peripersonal space, compared to extrapersonal space. Recent behavioral and neuroimaging studies with healthy individuals suggest the presence of a functionally homologous space coding system in humans (Bremmer et al., 2001; Holmes and Spence, 2004; Macaluso and Maravita, 2010; Pavani and Castiello, 2004; Spence et al., 2000; Spence et al., 2004). Moreover, there are reports of brain-damaged patients with specific impairments in detecting information within peripersonal space, but not extrapersonal space, or vice versa in extrapersonal space (Brozzoli et al., 2006; Cowey et al., 1994; Farnè et al., 2003; Làdavas and Farnè, 2004, 2006; Vuilleumier et al., 1998).

Studies in monkeys have shown that several parietal–premotor circuits work in parallel supporting sensorimotor transformation to control arm-hand movements in space. In fact, in the posterior parietal area PFG there are neurons that code not only for space, but are also active while the monkey executes a grasping action. In

* Corresponding author. Fax: +39 521 903900.
E-mail address: valentinasclafani@gmail.com (V. Sclafani).

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fact, about half of PFG neurons showing responses to visual stimuli moving in peripersonal space fired also during the active arm movement (Rozzi et al., 2008). Similar properties have been found in anatomically connected ventral premotor areas F4 and F5 (Maranesi et al., 2012). Other parietal cortical areas, located within the intraparietal sulcus (area AIP), possess neurons that are critically involved in grasping. For example, in both areas AIP and F5 there are neurons that have visuo-motor properties, firing both during the observation of objects and during grasping (Murata et al., 2000; Raos et al., 2006). Together, these and other investigations demonstrate the existence of several cortical parietal and premotor areas that code for several aspects of actions, and suggest that neuronal visual responses related to objects and space are tightly linked with the possibility of the body to move in space and to reach targets. These circuits have been proposed to play an important role in the organization of goal-directed movements in space, and lesions to these circuits can produce several impairments in visually-guided reaching and grasping (Fogassi et al., 2001).

The link between the control of movement and space perception has been emphasized by several neurophysiological and neuropsychological studies (Matelli and Luppino, 2001; Rizzolatti et al., 2002). Interestingly, space coding for peripersonal and extrapersonal space appears to be dynamic in that it can be modified by active movement and sensorimotor experience. For example, tool use can change the perception of the spatial relation between the body and the object upon which the tool is acting (Berti and Frassinetti, 2000; Berti and Rizzolatti, 2002; Halligan et al., 2003; Iriki et al., 1996; Longo and Lourenco, 2006; Maravita and Iriki, 2004; Maravita et al., 2002; Rizzolatti et al., 1983; Weiss et al., 2003). Another example is that of a patient affected by selective neglect for the space close to the body, whose symptoms were transferred into the far space after using an extension tool, as if the use of the tool remapped the far space as near-reachable space (Berti and Frassinetti, 2000).

Although developmental research on space coding is sparse, behavioral studies provide initial indications that young human infants have some spatial representation of peripersonal space when planning and executing reach movements (Clifton et al., 1991; Field, 1977). For example, 3-month-old human infants appear to encode locations egocentrically, showing initial evidence of a gradual shift from egocentric to object-centered references by 6 months (Gilmore and Johnson, 1997; Newcombe and Huttenlocher, 2003). It has been also reported that, between 4 and 5 months of age, human infants develop the ability to coordinate and update their spatial reference frames in relation to their capacity to lean the body forward towards objects (Yonas and Hartman, 1993). Moreover, 12-month-old human infants can use a tool to extend their spatial interaction range (McKenzie et al., 1993). Despite these studies highlighting important aspects of the development of space processing, the development of spatial discrimination – distinguishing peripersonal and extrapersonal space – remains largely unexplored.

Some studies have shown that infant macaques develop the capacity to reach and grasp starting from the third week of life (Lawrence and Hopkins, 1976; Nelson et al., 2011). In addition, other studies report that infant macaques' capacity to move autonomously in their surrounding environment is precocious, beginning in the first week of life (Hinde et al., 1964; Maestripieri, 1996). This suggests that the first weeks of life are critical for the development of body maps, which support infants' capacity to move in the environment and interact with objects. Although there is a strict dependence between the development of motor skills and space representation, the relationship between these two aspects of motor development has, to our knowledge, not been thoroughly explored. In the present study, we investigated the development of space processing in rhesus macaques between the second and the fourth weeks of life. Specifically, we presented infants with objects of different sizes at different distances from the body (i.e., peripersonal and extrapersonal space) and examined both the behavioral patterns used to reach objects and grip configurations for grasping objects.

A nonhuman primate model, and a macaque monkey model specifically, is advantageous for investigating the development of space perception. First, the neural mechanisms underpinning the control of reaching-grasping movement and space coding in humans and macaques are similar and have been described in great detail. In fact, homologous cortical areas control reaching-grasping and process peripersonal space in both species (Bremmer et al., 2001; Macaluso and Maravita, 2010; Pavani and Castiello, 2004; Spence et al., 2000, 2004). Second, given human infants' limited response repertoire in the first few months of life, it would be difficult to investigate the development of grasping in different space sectors. In contrast, macaques have a precocious motor development, making it possible to follow each infant's motor skill development, including their grasping and locomotion in relation to their perception of space.

Materials and methods

Pilot testing

Subjects and procedures

To develop a reaching-grasping task, we carried out a pilot study in the first and second weeks of infants' life, in which we tested 4 infants in their incubators, while still clinging to their surrogate, by presenting them with a large colored ball (21 mm diameter). We initially moved the ball both horizontally and vertically in front of them in order to evaluate the timing of the emergence of their ability to visually track the object and to adjust their posture. We then presented the ball in front of the infants and recorded any attempts to reach-grasp the target.

Preliminary behavioral observations

Preliminary observations revealed that from the fourth day of life all infants were able to visually track the moving object. Moreover, their capacity to cling firmly to the surrogate and move one arm in space to grasp objects improved in the first days of life, suggesting that in the first week of life important postural adjustment and coordinated visuomotor movements are emerging. However, their first attempts to reach and grasp the ball appeared only at day 7. In fact, starting from this age and across the second week of life, we scored a total of 81 reaching attempts, 51 (63%) of which ended with successful grips.

Based on these preliminary observations, we designed a task aimed at investigating the development of infants' capacity to perceive objects' size and space location.

Reaching-grasping task

Subjects and housing

Subjects were 16 infant macaques (*Macaca mulatta*), 10 males and 6 females, followed longitudinally from age 7–30 days (mean infant age: week 2 $M=10.19$ days, $SD=1.03$, week 3 $M=17.33$ days, $SD=.90$, week 4 $M=24.31$ days, $SD=1.11$). Infants were separated from their mother on day 1 post-partum and reared in a nursery facility according to procedures described by Shannon et al. (1998). Infants were individually housed in plastic incubators ($51 \times 38 \times 43$ cm) during the first two weeks of life, and housed in metal cages ($65 \times 73 \times 83$ cm) from the third week onward. Both housing arrangements contained an inanimate surrogate mother as well as