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A PERCEPTUAL-MOTOR MODEL FOR SPATIAL ORIENTATION OF SHAPES

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ABSTRACT: A model will be presented in which mirror image confusion is employed as an example of perception of shape orientation, occurring as a result of evolutionary change in vision and movement. In the most primitive condition, vertical and horizontal coordinates are absent and shapes are equivalent in terms of orientation. In this condition directionality in external space is not objectified and movement is reflexively toward or away from the visual target. In the second condition, only the horizontal axis is present. Changes in orientation from upward to downward are perceptually salient. Quadrupedal movement patterns and locomotion across land, dominated by the horizon, are associated with the evolution of a mammalian eye with enhanced acuity across the vertical axis. Vertical mirror image confusion ceases to exist. In the third condition, the vertical axis appears. Factors in primate evolution associated with the appearance of enhanced acuity along these visual axes are related to perception of lateral rotations. In the fourth condition, upright posture and development of lateral bias in eye movement are related to the human proclivity to differentiate right and left orientation of shapes while exhibiting increased difficulty in tasks that involve changes in the vertical orientation. Thus structural changes in evolution associated with posture and movement are demonstrated to account for differences in perceptual responses to orientation of shapes.

KEY WORDS: Perceptualmotor; Shape orientation; Evolution; Laterality; Posture.

Mirror image confusion is the tendency to have difficulty in learning the difference between shapes rotated 180 degrees on their own axes. Lateral mirror images are asymmetrical shapes rotated across their vertical axes, while vertical mirror images are shapes rotated on their horizontal axes. The perceptual phenomenon of lateral mirror image confusion (difficulty with shapes rotated left or right rather than up or down) is of interest in the study of the evolution of visually guided behavior because lateral mirror image confusion is evident in many species, including octopus (Sutherland, 1957), rats (Kinsbourne, 1971), cats (Parriss, 1964), ferrets (Wight, Milliken, & Ward, 1988), bushbabies (Sanford & Ward, 1986), and monkeys, (Riopelle, Rahm, Itiogawa & Draper, 1964), as well as in human children (Bryant, 1969). It is notably absent in most intact human adults. There have been attempts to explain the absence of lateral mirror

image confusion in humans in terms of their learned ability to read left to right and thus make discriminations based on verbal rules differentiating right from left facing characters (b from d). More neuro-behaviorally oriented explanations account for lateral mirror image confusion, or its absence, in terms of cerebral asymmetries, (see Corballis, 1983). However, it is of interest to think of mirror image confusion as an example of the perception of orientation in extrapersonal space, and consider how and why this sort of perceptual response might change along evolutionary lines.

Over the past few years there has been a renewed interest in motor theories about perception (see Schierer, 1987). Recent investigations with human subjects have demonstrated the role of movement bias and postural adjustment in visual judgment of line length and directionality (Coren, 1986), circle size (Coren, Bradley, Hoeng, & Girgus, 1975), shape identification (Rock, 1974), and tactuospatial learning (Ward, Alvis, Sanford, Dodson, & Pusakulich, 1989). From a comparative point of view, one is compelled to wonder how changes in sensory and motoric factors, under the pressures of environmental adaptation, might influence the nature of an animal's perceptual world. In this paper, we will present a model, based upon data relevant to mirror image confusion. This model demonstrates how the structure of the visual apparatus as well as the structure of the body itself might determine factors relative to how objects are perceived to be oriented in space.

The first step in this model, depicted in Figure 1a, is a blank field. Notably absent are the axes marking any vertical or horizontal coordinates, so that this two dimensional field is essentially directionless. This is the baseline of the model. If the letters b, d, p, q, representing visual targets, are superimposed on this field, there would be no way to discriminate them visually. In a directionless field they would be identical.

Mach (1987) long ago observed that a perfectly symmetrical organism would have total mirror image confusion. We have no data concerning such an organism. What needs to be considered is the nature of the living animal's perceptual field relative to the salience of orientation of objects within that field. A simple example is found in the visually guided behavior of the salamander. If the eyeball of the salamander is rotated 180 degrees on its optic axis, it will heal in position. The retina is then turned upside down and right to left. The result is that all visuo-motor responses toward prey are reversed. It will continue this backward behavior until starvation (Sperry, 1943). The relationship between the salamander's visual space and the environmental space in which it operates is fixed. Right, left, above or below have no objective significance, since as demonstrated experi-

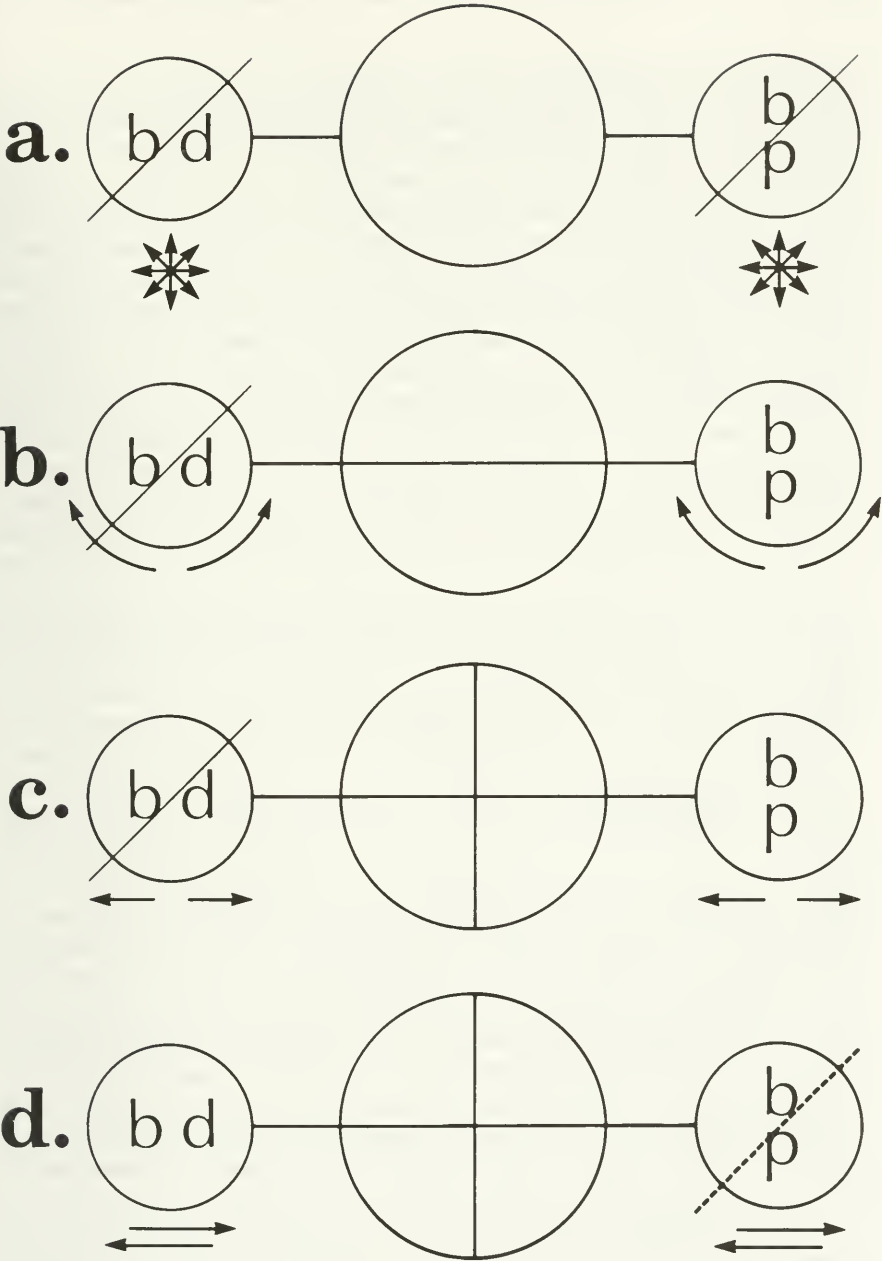


FIGURE 1. Diagrammatic representation of the model. Central circles represent visual fields with horizontal and vertical meridians indicated. Mirror image pairs are within peripheral circles for each visual field. Pairs which cause confusion are marked with cross bars. Dashed lines indicate a partial or questionable state. Arrows represent directionality in inspection.

mentally, its responses are determined by stimulation of retinal points, not by its actual relationship to objects in space. Another example is found in an animal that normally does show mirror image confusion, for lateral but not up-down rotations (Sutherland, 1957). The octopus has a nervous system that is radially symmetrical. Because it feeds while clinging to objects in the water, whether upside down or horizontally positioned, the octopus is often in a strange relation to gravity. To compensate for its seeming disregard of up and down, the octopus eye is structured so that it rotates relative to gravitational down. It has been demonstrated that if the vestibular pathway controlling eye movement is lesioned, the eye no longer responds as described and the octopus loses all learned ability to make a vertical mirror image discrimination (Young, 1971). In the baseline condition of our model, as for the lesioned octopus, right, left, up and down are equivalent. Both lateral and vertical mirror image confusion are the rule.

The second condition, seen in Figure 1b, represents a visual field with only one axis, the horizontal meridian. If the letter b is rotated 180 degrees across the horizontal meridian, it becomes p. When the difference between b and p is appreciated, a vertical mirror image discrimination has been made. Thus an organism to whom up and down, top and bottom of objects in the environment are behaviorally meaningful would implicitly structure visual space about this axis. But what is the behavioral significance of the horizontal axis? When an animal moves on four legs across the land, following and watching its prey or its enemies, it is dependent for survival upon their movement patterns as much as its own. Changes in landscape are critical for movement. The horizon itself is the most basic referent for vision. The salience of the horizontal plane to vision is imprinted even in the structure of the eye. For example, the Mongolian gerbil, a small rodent living in a flat, arid environment, has its highest acuity along the horizontal axis of the retina (Baker & Emerson, 1983). If such a case is considered to be a minimal structural condition for the visual adaptation of a free-ranging ground mammal to its environment, it is little wonder that vertical mirror image confusion would not exist at this level.

But what about lateral mirror image confusion? In Figure 1b, where there is absence of a vertical meridian, if b and d are represented, they are the same, since d is simply b rotated on its own vertical axis. If lateral mirror image confusion is a result of the absence of a vertical axis in the perceptual field, as the model would have it, what would we need to consider in the behavior of animals to support the model?

Although much is known about visual capacities of animals, less has been said about how they inspect objects in order to learn some-

thing about them. It is important to consider the structure of the animal as well as the behavior. For most non-primate mammals, the eyes are laterally placed, offering a wide breadth of view. With foveal vision absent, lateral excursion of eye movement is limited, and movement of the head, as well as movement in space, takes precedence. The non-primate, without hands to manipulate objects for inspection or to bring them closer to view, is more dependent upon its own movement toward and around objects as an inspection strategy. Our own observations are that while dogs or cats (predators) will quietly gaze at an object awaiting its movement, they inspect by such behaviors as headcocking, or moving about the object of interest. Rats, learning to discriminate two dimensional forms from a distance, make repetitive, back and forth movements before the task is achieved. The tree shrew, in the same situation, weaves wild figure eights with its body as learning is accomplished. In short, when visual inspection is tied closely to movement of the body, the right and left halves of space relative to some critical axis are perhaps not so important for visual learning. For a quadrupedal animal the plane of movement is predominantly on the horizontal. If one moves around the b and the d horizontally, they become interchangeable. If one moves around a saber toothed tiger, he is the same tiger on either side. If on the other hand, his feet are in the air, or worse, if yours are, the world begins to look a bit different. In Figure 1b, lateral mirror image confusion exists, but vertical mirror image confusion does not.

In the third condition, Figure 1c, the vertical axis appears. Now space is divided into right and left halves in which the d points left but if rotated on the vertical axis becomes b, pointing right. Again, structural considerations are important in applying the model to animal vision. Both the evolution of the eye as well as changes in posture and limb use separate the primate from the non-primate quadruped. In primates, who have enhanced specialization of central vision, the retinal areas of sharpest acuity occur along both the horizontal and vertical axes of visual space (Simeonova & Vassilev, 1985; Vandebusshe & Orban, 1983). Thus, this condition can be thought of as representing a primate visual field. Wight et al (1988) have pointed out that the significance of the vertical meridian in vision appears to increase in the primate order as bipedalism begins to appear in mammals. It is an interesting thought that as the neuraxis becomes more vertically oriented, as the upright posture in locomotion evolves, the retinal structure also develops in such a way as to fine tune to the vertical dimension of space. As the forelimbs are freed from the reflexive constraints of locomotion, they become increasingly independent from each other. Also, with the evolution of the hand, the differentiation of the two halves of the body along the neuraxis give the

right and left halves of internal space a behavioral significance to the primate that is lacking in the quadruped. Thus, perception of internal space, the division of the body into distinct and independent halves along the neuraxis, is reflected by a perception of external space in which right and left halves also exist visually.

But how do these evolutionary changes relate to the perception of orientation and to mirror image confusion? Once the vertical axis is established, the lateral mirror images *b* and *d* can be inspected in one of two ways, medially to laterally, as diagramed in Figure 1c, or from one pole of the horizontal axis to the other as in Figure 1d, right to left or left to right. The perceptual result is quite different, for with medial to lateral inspection *b* continues to equal *d*. It is only with a consistent lateral bias in the sequence of movement that lateral mirror image confusion disappears. Let us assume that the medial to lateral inspection represents the condition found in such primitive primates as the bushbaby, or the monkey, who can learn a lateral mirror image discrimination but with considerable difficulty (Sanford & Ward, 1986) while the right to left, left to right sequence represents the adult human who makes these discriminations easily. Prosimians and simians show far less independent use of each hand than humans. They also utilize the four limbs in locomotion such that bilaterally symmetrical or coordinated movements occur more frequently. For completely bipedal man with a highly independent use of two hands, there is a significant increase in movements not coordinated toward and away from the midline axis of the body. Thus the internal representation of the right and left halves of space gain increasing importance.

A second factor related to visual and somatic structure is equally important. In non-human primates, lateral excursion of the eyes is much less than for humans. Consequently, scanning across the visual field for the non-human primate is more dependent upon moving the head, an activity directed away from the midline of the body, medial to lateral. For humans, eye movements clearly exhibit a lateralized directional bias for inspection. Inspection of a complex visual array begins by entering the target on the left and moving rightward (Standing, Conezio, & Haber, 1970). In keeping with our model this consistent bias in sweep differentiates primates who show lateral mirror image confusion from those who do not. A medial to lateral head movement is the mode for the more primitive primates and possibly for children (Gesell & Ames, 1947; Coren, Porac, & Duncan, 1981). For humans, the lateralized scan, facilitated by wide lateral excursion of the eyes, promotes a consistently directional eye movement sequence. In fact, it has been demonstrated that individuals with visuospatial dyslexia, who tend to reverse words and letters, like a child learning to read, often show unusually erratic eye movements

while reading (Lesévre, 1968; Zangwill & Blakemore, 1972), and have difficulty tracking right-left or left-right light pattern sequences (Pavlidis, 1981).

Non-human primates, with a more vertical neuraxis than other mammals, do, like quadrupeds, exhibit lateral mirror image confusion, but, according to our model, for a different reason and possibly to a lesser degree. Bipedal man does not. But as the vertical axis gains salience, there appears to be a perceptual trade-off. This condition is represented in Figure 1d. It appears that humans, unlike any other mammals for whom data exists, suffer from vertical mirror image confusion. Rock (1974), has demonstrated that while subjects were easily able to identify familiar shapes, such as a map of Africa, as flipped from right to left, when the same map was turned upside down, it was not recognized. He attributed this to a tendency to assign a natural base to objects. Using a long series of abstract designs with no semblance of a natural base, we have found that although right-left reversals were recognized (although with some difficulty), vertical rotations were significantly more difficult (Sanford, 1986). This is not the case in any data from studies of animals or children in which the vertical rotation is used as a comparison, but supports data which shows that adult human subjects are slower to respond when differentiating the poles of horizontal axes (east versus west) than those of the vertical (north versus south) (Scholl & Egeth, 1981).

In summary, a model in which mirror image confusion has been presented, as an example of perception of shape orientation, occurs as a result of evolutionary change in vision and movement. In the most primitive condition, vertical and horizontal coordinates are absent and shapes are equivalent in terms of orientation. In this condition, directionality in external space is not objectified and movement is reflexively toward or away from the visual target. In the second condition, only the horizontal axis is present. Changes in orientation from upward to downward are perceptually salient. Quadrupedal movement patterns and locomotion across land, dominated by the horizon, are associated with the evolution of a mammalian eye with enhanced acuity across the vertical axis. Vertical mirror image confusion ceases to exist. In the third condition, the vertical axis appears. Factors in primate evolution associated with the appearance of enhanced acuity along these visual axes are related to perception of lateral rotations. In the fourth condition, upright posture and development of lateral bias in eye movement are related to the human proclivity to differentiate right and left orientation of shapes while exhibiting increased difficulty in tasks that involve changes in the vertical orientation. Thus structural changes in evolution associated with posture and movement are demonstrated to account for differences in perceptual responses to orientation of shapes.

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