

New aspects of motion perception: selective neural encoding of apparent human movements

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Perception of apparent motion operates somewhat differently for objects and human figures. Depending on the interstimulus interval, the latter may give rise to either perception of a direct path (i.e. biologically impossible) or indirect path (i.e. biologically possible). Here, PET was used to investigate whether a change in brain activity accompanies this perceptual shift. We found neural encoding of apparent motion to be a

function of the intrinsic properties of the stimulus presented (object vs human) as well as the kind of human movement path perceived (biomechanically possible vs impossible). Motor and parietal cortex were only involved for possible motion which suggests that these regions are selectively activated to process actions which conform to the capabilities of the observer. *NeuroReport* 11:109–115 © 2000 Lippincott Williams & Wilkins.

Key words: Apparent motion; Inhibition; Possible vs impossible movement; Primary motor cortex; Simulation; V5/MT

INTRODUCTION

Visual perception of apparent motion results from the sequential presentation of static objects in different spatial locations. For example, the perception of fluid motion arises from the rapid display of the static frames of a film. Apparent motion is a robust visual effect; objectively static objects appear to move across 2D and 3D space [1,2] and over a wide range of stimulus presentation rates, known as stimulus onset asynchronies (SOAs) [3]. The traditional explanation of this phenomenon is that the visual system is biased toward selecting the simplest interpretation of the image. A fundamentally important characteristic of classical apparent motion studies is the finding that object identity does not influence the motion perceived since objects appear to move along the shortest or most direct path [4]. In Kolers' terms, motion dominates the perception and the figure is dependent on the motion [5]. However, more recent investigations suggest that perception of apparent motion operates somewhat differently when the object presented is a human figure [6–8]. Shiffrar and Freyd found that as SOA increases (>400 ms), observers become increasingly likely to report seeing indirect but biologically possible paths of apparent motion rather than the shortest paths. For example, observers perceive arm

movement around a head when the presentation of a static photograph of a model with her right arm positioned behind her head is followed 450 ms later by a second photograph of the same model with her right arm positioned in front of her head. In contrast, with short SOAs (<300 ms), observers report seeing the shortest or most direct movement path even when that path requires a biologically impossible action. Thus, if the right arm is shown behind the head and then 50 ms later is shown in front of the head, the arm appears to move directly through the head. This perceptual shift (between perception of impossible and possible human action paths) challenges the traditional view of apparent motion by demonstrating that, at some time intervals, object structure can affect movement path perception.

The goal of the present investigation was to determine whether the perception of biologically impossible and possible apparent human movements are mediated by distinct brain regions, even though the stimulus features are the same and the experience of an apparent motion occurs in both cases. We used PET to measure changes in regional cerebral blood flow (rCBF) during perception of possible versus impossible apparent human movements. A classically derived object apparent motion task and a static

presentation of object and human figures were used as control conditions.

Previous studies examining the neural correlates of apparent motion have found that apparent motion, analogous in experience to real motion [9], selectively activates area V5/MT [10–12]. Accordingly, we anticipated activity in this region during each of the apparent motion conditions. Because MT is the singular, primary brain region associated with the phenomenon to date, we were especially interested in whether differential patterns of activation would emerge in the two human apparent motion conditions. A number of studies have demonstrated that motor planning regions respond during the processing of perceived, imagined and real action [13–15], and we wondered if the same would be true when apparent possible human movements were perceived. Moreover, the extent to which such activation may be linked to the physical limitations of human movement has not been considered. Using the apparent motion paradigm to exam-

ine the neural correlates of perceiving 'impossible' apparent human actions provided a means to address the issue.

MATERIALS AND METHODS

The stimulus set generated was similar to that used by Shiffrar and Freyd [6] (see Fig. 1). On each trial, stimulus figure pairs (object or human) were alternately presented for 6 s. Stimulus presentation rates differed across conditions: for condition P, static pictures were presented at a rate of 1.3 Hz (SOA = 750 ms; stimulus duration (SD) = 400 ms; interstimulus interval (ISI) = 350 ms), for condition I pictures were presented at 4 Hz (SOA = 250 ms; SD = 150 ms; ISI = 100 ms), and for condition O, half of the pairs were presented at 1.3 Hz and half were presented at 4 Hz. Following stimulus presentation, a forced-choice response task displayed two paths of movement. One path outlined the most direct movement path and the other outlined an indirect path which conformed to the constraints of the stimuli presented. Subjects responded by depressing either

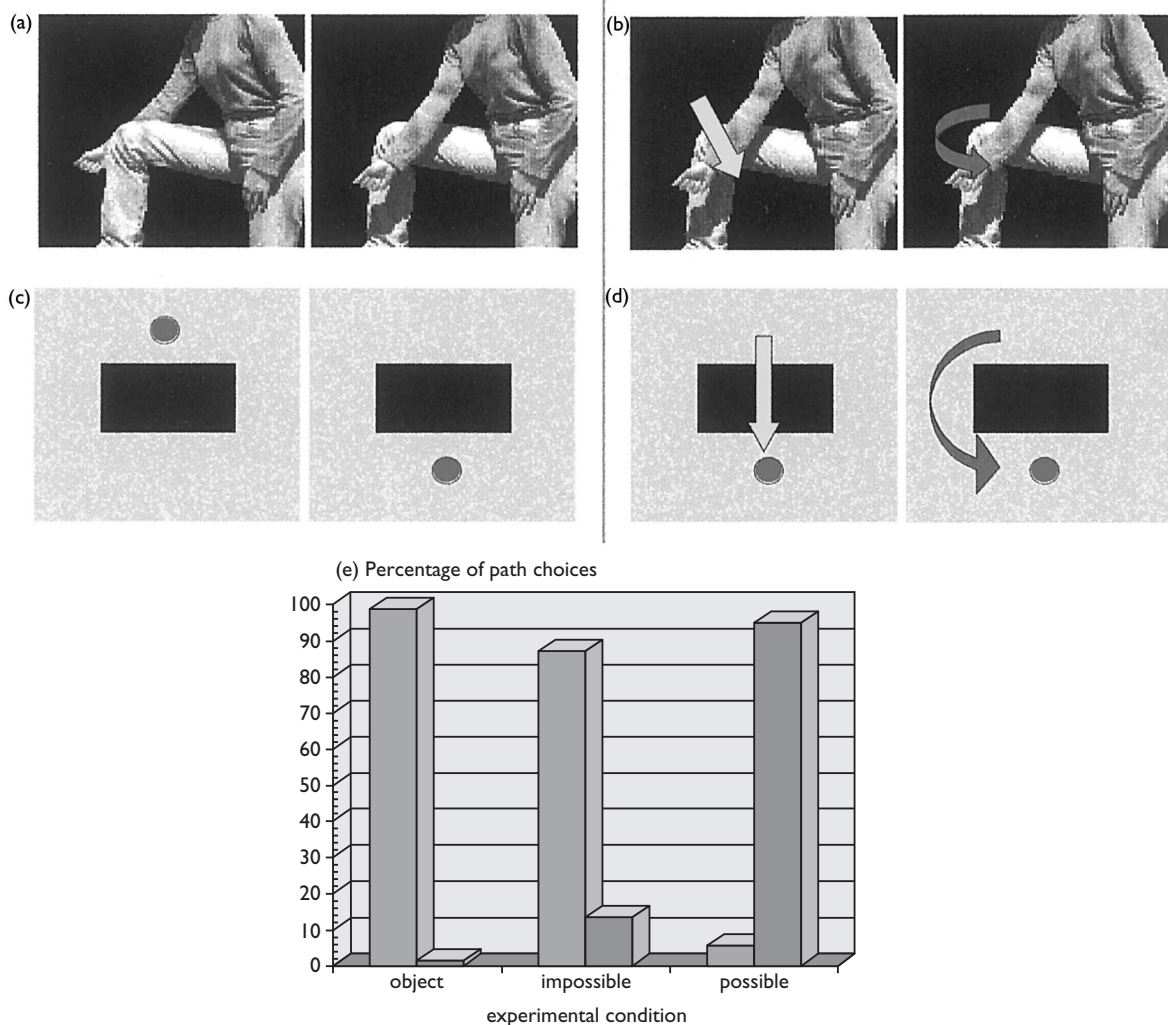


Fig. 1. Experimental paradigm. 18 pairs of different human figure stimuli (A) were created in which the difference between the two pictures was only in the placement of the right limb. The same human figure pairs were used in both conditions P and I. The 18 object stimulus pairs used (e.g. C) were computer generated so that one 2D element changed position between the two pictures. Following stimulus presentation, a forced-choice response task displayed two paths of movement. One path outlined the most direct movement path (B, left and D, left), and the other outlined an indirect path but one that conformed to constraints of the stimuli presented (B, right and D, right).

a left (with their right hand index finger) or a right (with their right hand middle finger) key. Direct and indirect movement path outlines appeared on the right and left sides of the forced choice display at random.

Brain activity was measured across three apparent motion conditions: human possible (P), human impossible (I), and object (O). Presentation of human and object figures was used for a static perception control (condition C). Each of the four conditions was replicated three times during a single PET session in order to improve the statistical power, for a total of 12 scans per subject. Order of conditions were counterbalanced across subjects so that no two subjects received the same order and no two consecutive scans were of the same condition. During each scan, subjects completed a total of 18 trials beginning 10 s before injection and lasted ~120 s. The integrated counts were collected for 60 s, starting 20 s after the injection time, were used as an index of rCBF.

Ten males (21–28 years old) gave their informed consent to participate in the experiment and were paid for their participation. The experiment was performed in accordance with guidelines from the declaration of Helsinki and with the approval of the local Ethical Committee (Centre Léon Bérard). Subjects were examined in the supine position on the bed of the PET scanner. Changes in rCBF were measured using the intravenous radioactively labeled water ($H_2^{15}O$) bolus method. Control of head position throughout the PET session was made by laser alignment along with reference points on Reid's line before and after each session. The PET camera was a Siemens CTI HR+ (63 slices, 15.2 cm field of view) with collimating septa retracted, operating in high-sensitivity mode. rCBF was estimated by recording the radioactivity following the intravenous bolus injection of 333 Mbq [^{15}O]H $_2$ O through a forearm cannula placed in the brachial vein.

All voxels were submitted to an ANOVA and only those voxels found to be significant ($p < 0.05$) were submitted to principal component analysis and canonical variate analysis (CVA). The statistical parametric mapping technique (SPM 96) with software provided from the Wellcome Department of Cognitive Neurology, London, UK and/or procedures implemented in MATLAB (Mathworks Inc., Sherborn MA, USA). The scans from each subject were realigned to a canonical image, transformed into standard stereotaxic space [16] and smoothed using the standard image furnished with the SPM software as reference. The images were then smoothed using an isotropic Gaussian kernel with a full width at half-maximum of 10 mm in all dimensions. Changes in global blood flow were corrected by proportional scaling.

The preprocessed data were subjected to ANCOVA with the three tasks as a factor of interest and the subjects as a factor of non-interest. The two factors were considered fixed by SPM; when the factor subject was considered as a random factor, the same results emerged. For 36 113 voxels (a subset of the voxels from the entire image) an $F(2,78)$ value of 3.11 (testing the null hypothesis that including the effects of interest does not reduce the error variance) corresponded to a probability level of erroneous decision < 0.05 . These voxels were submitted to further analysis. Task-specific effects were evaluated using contrasts of the parameter estimates leading to a t value (which has a

Student's t distribution). SPM{ t s} were then transformed to a SPM{ Z } and the significance of clusters was based on the theory of continuous, strictly stationary, stochastic Gaussian random fields.

RESULTS

The behavioral responses obtained during the PET session replicated the pattern of results found by Shiffrar and Freyd [1]. Indirect, biologically possible movement paths were perceived when human figures were presented at long SOAs (condition P), while direct, physically impossible movement paths were perceived when the same human stimuli were presented at short SOAs (condition I). In contrast, subjects consistently reported seeing the most direct paths of movement when inanimate objects were presented (condition O), regardless of SOA (see Table 1).

An *a priori* canonical variates analysis (CVA) was run and revealed two linear effect components underlying overall differences in activation in the three apparent motion conditions (Fig. 2). For this analysis, the dimensionality (number of components or voxels) of the data was reduced to a number smaller than the total number of observations and the image data were then transformed to a set of orthogonal principal components. The two linear combinations of the components presented here resulted in three clusters that precisely corresponded to the three activation conditions. Each of the 10 symbols within each cluster corresponds to a single mean value for each subject.

Table 1. Mean percentage of path choice (direct vs indirect) for each of the three apparent motion conditions

	Object	Human possible	Human impossible
Direct	98.7	5.2	86.9
Indirect	1.3	94.8	13.1

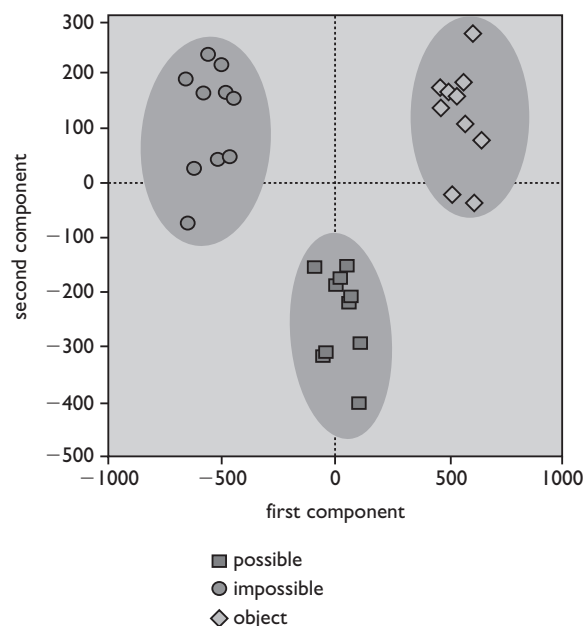
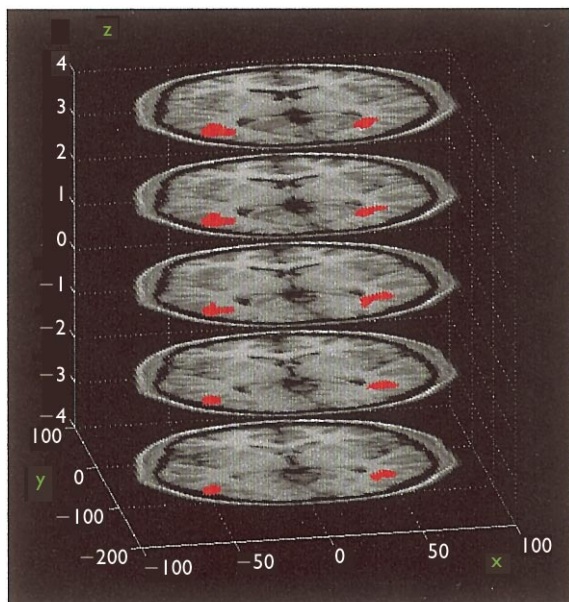
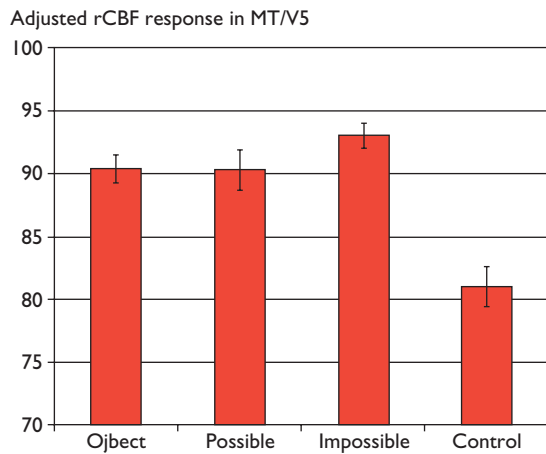


Fig. 2. Canonical variates analysis (CVA).

The second component (y-axis, mean value of $O = 528$, $I = -546$ and $P = 17$) outlines a difference between possible human movement and object/impossible human movement, reflecting an overall difference in activation between the visual perception of direct and indirect movement paths. The basis of first component is less evident (mean value of $O = 126$, $I = 114$ and $P = -241$), but may reflect an effect of attention.

Activity of area V5/MT was indeed significant across each of the three apparent motion conditions (Fig. 3); however several brain regions of interest were also selectively activated during the two different human movement conditions (Table 2). When subjects perceived possible paths of apparent human movement (compared to perceiving biologically impossible apparent movements, contrast P-I), the most significant bilateral rCBF increase



- Left V5: $-44, -70, 0 \pm 27$ mm
- Right V5: $+40, -68, 0 \pm 18$ mm

Fig. 3. Significant activation of area V5/MT is each of the three apparent motion conditions.

Table 2. Significant activations during visual perception of biologically possible (contrast P-I) and impossible (contrast I-P) human apparent motion

Brain region	Stereotaxic coordinates		
Contrast P-I			
L Superior parietal	-12	-52	68*
R Superior parietal	20	-56	66**
R Primary motor cortex	28	-28	64**
R Superior frontal gyrus	12	-4	58**
L Primary motor cortex	-24	-22	58**
L Superior frontal gyrus	-20	38	30*
R Cingulate gyrus	2	14	26*
L Superior temporal gyrus	-62	4	2*
R Thalamus	14	-16	2*
R Putamen	30	-2	-2**
R Superior temporal gyrus	50	-8	-2*
R Cerebellum	26	-34	-22*
L Cerebellum	-48	-60	-42*
Contrast I-P			
R Postcentral gyrus	42	-34	60**
R Inferior frontal gyrus	42	32	10*
R Cuneus	14	-98	0**
R Lateral orbital gyrus	28	22	-8**
R Middle temporal gyrus	68	-12	12**
L Middle orbital gyrus	-12	38	-16*
L Inferior temporal gyrus	-52	-26	-20*
R Inferior temporal gyrus	44	-6	-30*

** $p < 0.0001$; * $p < 0.001$

($p < 0.001$) was found in the primary motor cortex (Fig. 4A). Significant bilateral activations were also found in the superior parietal gyrus, superior frontal gyrus, superior temporal gyrus and the cerebellum. A unilateral right activation was found in the putamen, cingulate gyrus and in the thalamus.

An intriguing different pattern of activation emerged when the possible and impossible human apparent movement conditions were compared (contrast I-P). Of particular interest, the right lateral orbital gyrus (BA 47) and left medial orbital gyrus (BA 11) were activated (Fig. 4b). There was also significant activation in the inferior temporal gyrus in both left and right hemispheres. The greatest activation was found in the cuneus which may reflect the rapid stimulus presentation rate used in this condition. Unilateral activations were also found in the right inferior frontal gyrus, left middle temporal gyrus, and the left cerebellum. Thus, no significant motor or parietal cortex activation was found during the visual perception of impossible human movement even though identical human figure stimuli were displayed in both conditions P and I.

DISCUSSION

The selective activation of ventral prefrontal cortex during the perception of impossible human movements probably reflects subjects' detection of deviations from normal motor action paths. Significant activation in this region has been found during perception of violations in visual task outcomes [17] and when subjects plan for but then subsequently inhibit themselves from completing physical action [18]. Evidence for the role of this region in monitoring information and inhibiting normal or expected responses

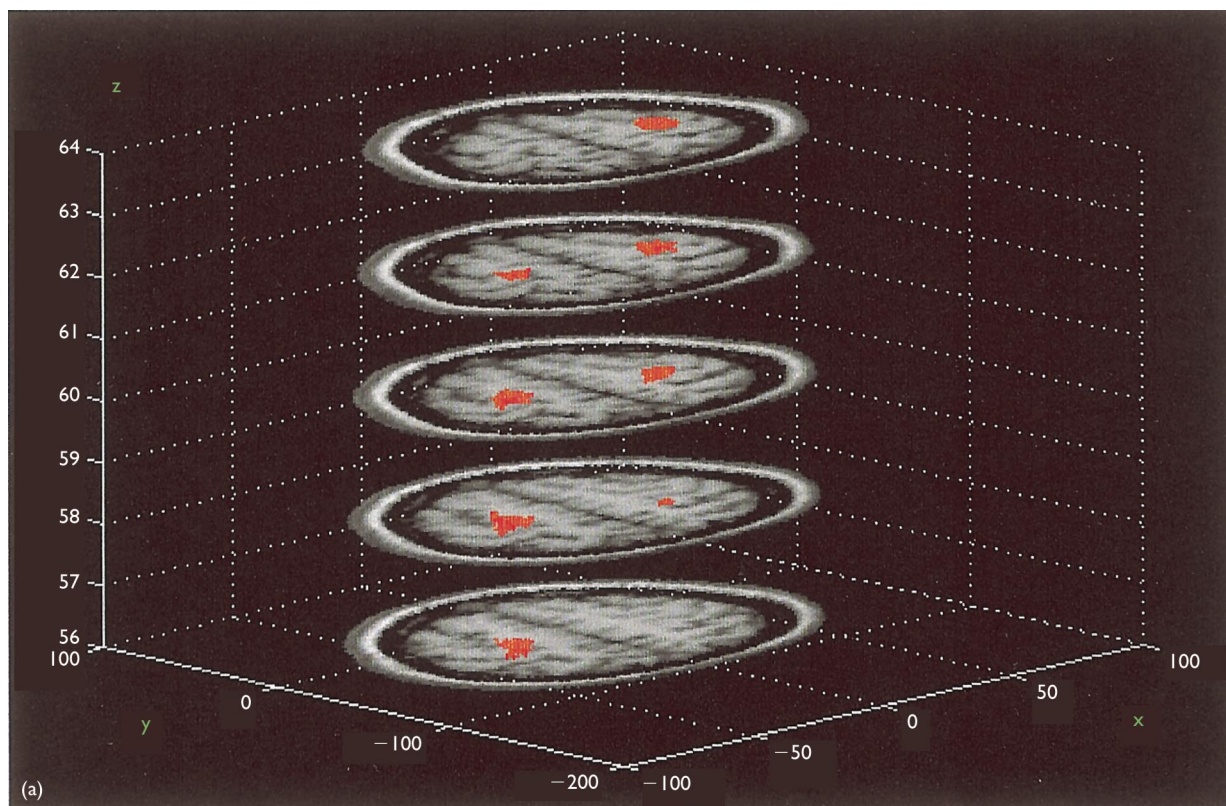


Fig. 4. Regions of interest. Bilateral activations in primary motor cortex found during visual perception of humanly possible apparent movement paths (**A**), and the right hemisphere activation in orbital frontal cortex during visual perception of impossible human apparent movements (**B**). PET data were reconstructed here into an orthogonal 3D space using stereotaxic coordinates.

has been reported in both healthy [19] and patient populations [20]. The prefrontal lobe activity we found during perception of impossible human movements offers further support for the hypothesis that this region mediates attention in a top-down fashion by filtering out irrelevant information [21].

Our results demonstrate that visual perception of apparent human movement selectively activates motor and sensory regions of the brain, however this pattern of activity only emerged when the actions perceived were humanly possible. Recall that the same stimulus set and perceptual process were present in both of the human apparent motion conditions. Apparent motion is a unique case because motion is perceived even though none is explicitly imagined, executed, or presented. However, if physical motion is never explicitly presented, how might a motion percept be generated?

There is some evidence that apparent motion impressions involve an explicit representation of movement, much like that which occurs during motor imagery. For example, the timing of apparent motion and an imagined object rotation is similarly chronometric [2] and processing of visual information is significantly delayed if it lies on (*vs* off) an apparent motion path [22]. This latter result suggests that there is an explicit filling-in, or simulation, of movement. Imagined movements are, likewise, mentally simulated and the brain regions activated during mental movement tasks depend on the nature of the movement generated. For example, motor imagery tasks selectively

activate motor-specific brain regions such as M1 [23], while the processing of visual images is generally restricted to visual mechanisms [24]. The superior parietal lobule has been found to play a critical role in maintaining internal representations of the body [25] needed for motor planning [26,27]. The activation of motor and parietal cortex during condition P suggests that perception of apparent human movement, just as imagined human action, is processed in ways analogous to real action: the movement paths followed and the neural encoding underlying each are quite the same. However, these two processes may not be entirely equitable: imagery is a top-down or cognitively driven phenomenon while apparent motion is a bottom-up or perceptually driven phenomenon. Studies explicitly comparing the neural circuitry underlying these two processes are needed before a more definitive relationship between the two may be drawn.

The absence of significant activation in motor and parietal cortex during the visual perception of impossible human movement suggests that these regions are selectively activated to process actions which conform to the capabilities of the observer. So while these brain regions seem to be intimately tied to the processing of human action, it appears that this relationship holds only when the movements are biologically possible. We might expect an absence of motor executive activations during the visual perception of actions that an observer interprets as beyond his/her motor capabilities, e.g. a technically challenging ballet movement. In such cases, the impossibility of com-

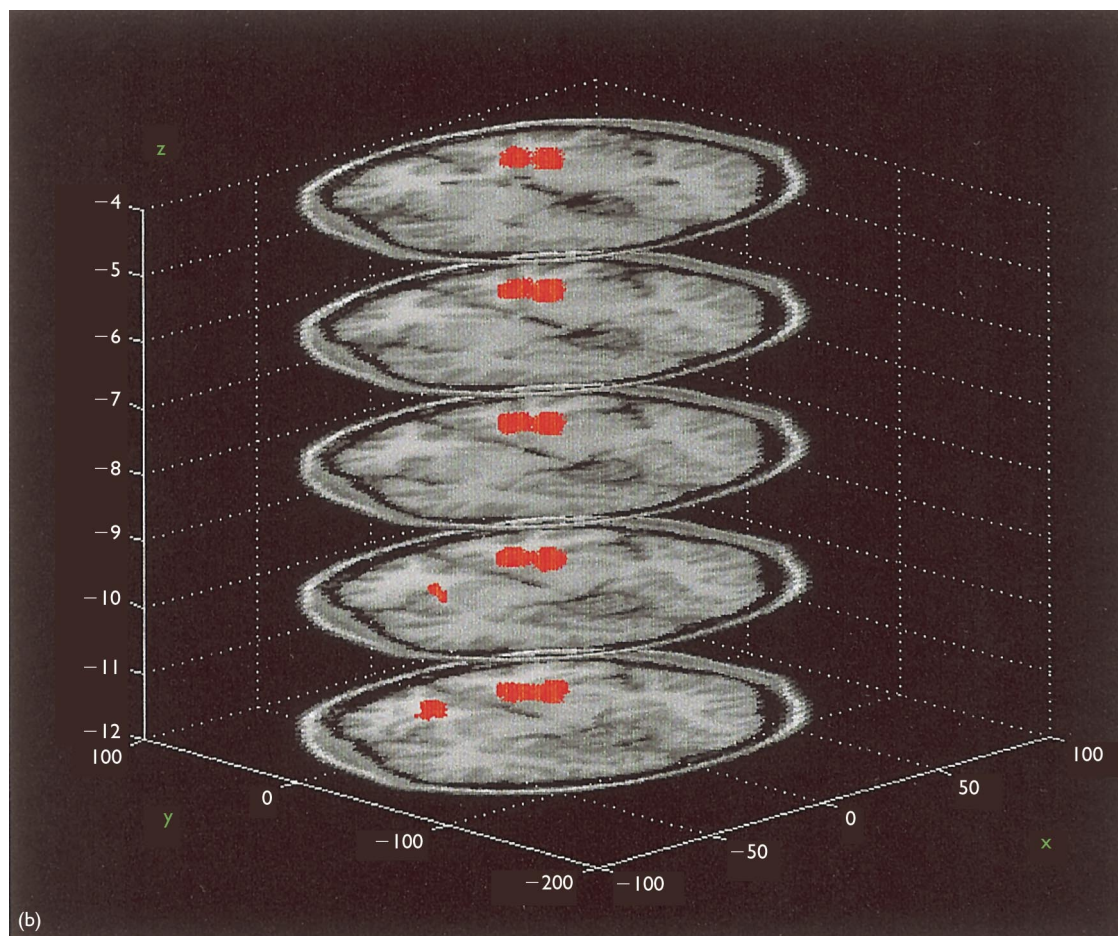


Fig. 4. (Continued).

pleting the action is determined within the context of the observer's own motor experience rather than in terms of the general movement limitations of the human body as was the case for the impossible actions perceived in our study.

CONCLUSION

The present investigation provides the first evidence that the neural correlates of apparent motion perception extend beyond visual cortex. Apparent motion has been studied for decades. The classical interpretation of this phenomenon is that the visual system prefers to see the simplest things. But what is 'simple'? Many previous studies have demonstrated that when an object appears and then reappears in a second location the default perception is of an object traversing space over the most direct line between the two points. When a human figure is presented, the simplest perception appears to be direct motion when time is quite limited. When more time is provided, however, an indirect or natural action path is visually perceived. Perhaps possible action paths are not seen at short intervals because the motor cortex requires more time to activate and interpret. Further investigations which include a temporal analysis of the motor and orbitofrontal cortex activations are needed. At present, we speculate that

natural actions paths are more likely to be seen at time intervals in which the action could actually be executed.

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