item was stored (left or right sides); and (3) 'when' (4 h or 124 h ago) the worms were cached. Current theories of human episodic memory refer to autonoetic consciousness— the conscious experience of self—that accompanies episodic recall but, as this state has no obvious manifestation in non-linguistic behaviour it is probably undetectable in many species. In terms of purely behavioural criteria, however, the cache recovery pattern of scrub jays fulfills the three, 'what', 'where' and 'when' criteria for episodic recall and thus provides, to our knowledge, the first conclusive behavioural evidence of episodic-like memory in animals other than humans.

Methods

Subjects. Adult, hand-raised scrub jays, which were allocated randomly to the Degrade (n = 8), Replenish (n = 8) and Pifler (n = 7) groups, were maintained under the same conditions as in the previous studies in which they had participated. Six birds (Degrade, n = 3; Replenish, n = 1; Pifler, n = 1) that failed to store at least one item of both food types during the test trials were omitted from the analysis.

Training and testing. The birds were deprived of their maintenance diet for 4 h before each caching phase of the 4-h and 124-h trials (Fig. 1), and during the 4-h retention interval between the second caching phase and recovery. At the start of each caching phase, a storage tray was placed in the bird’s home cage together with a bowl of 30 shelled peanuts or wax worms for 15 min. To provide a storage site that was unique and discriminable on every trial for each bird, the storage tray used on a particular trial was drawn from a large set of sand-filled plastic ice-cube trays (2 × 7 array of 2.5-cm cube molds), each rendered visuospatially distinct by a surrounding structure of Lego bricks. Access to one side of the storage tray during the first caching phase and the other side during the second caching phase was prevented by a clear Perspex cover. At the end of each caching phase, the number and location of caches were recorded before the food items were removed from the tray. Before each 15-min recovery phase, peanuts were placed in the same ice-cube molds in which they had been cached on the training trials. On 4-h training trials, wax worms were also returned to their original cache locations. On 124-h training trials, decayed worms were placed in those sites for birds for the Replenish group. The worm sites remained empty for the Piflered group. Furthermore, before all recovery phases the sand substrate was replaced to remove any local visual cues about the location of caches. The procedure was the same on the test trials, except that none of the caches was returned to the storage tray before the recovery phase. The order of the 4-h and 124-h training and test trials was counterbalanced across birds within each group, as was the side of the storage tray in which peanuts and worms were cached. To minimize observer bias, different observers recorded the behaviour during the caching and recovery phases so that the observer, during the recovery phase was unaware of the treatment received during caching.

Pretraining. Before the training and test trials, all birds received at least four pairs of pretraining trials. The procedure during pretraining trials differed from that during training trials in three respects. (1) On pretraining trials, peanuts and worms were cached in separate, visuospatially distinct, trial-unique storage trays. Thus during cache recovery, birds were presented with a choice between the two trays on pretraining trials. (2) The second caching phase of a pretraining trial followed immediately after the first one. (3) The cache recovery phase occurred 4 h after the second caching phase on one trial of each pair of pretraining trials and 124 h later on the other pretraining trial. The order in which peanuts and worms were cached was counterbalanced within groups, as was the order of the 4-h and 124-h trials within each pair of pretraining trials.
reached the targets with an average IAI of 5 and 15 ms (s.d., 106 and 125 ms). These IAIs are much shorter than required for successful performance, indicating synchronization of the movements of the hands.

We recorded single-unit activity from homologous sites in the two hemispheres during task performance. We analysed the activity of 189 neurons that were within the arm area of MI (72 from monkey F and 44 from monkey G) and SMA (73 from monkey F).

Most MI cells (62%, 72 of 116) were directionally selective (see Methods) during unimanual movements of either the contralateral or ipsilateral arm. Table 1 shows that, although many of these neurons (29%, 21 of 72) were activated in relation to movements of both arms, modulation in contralateral movements was stronger in 73% (53 of 72) of the responsive cells. In contrast, directionally selective units in the SMA (59% of the cells, 43 of 73) were distributed evenly between the two arms.

Cell activity revealed bimanual-related components of activity (Figs 2 and 3). Figure 2 shows the activity of a neuron recorded in the right SMA. It was inactive in unimanual movements towards 45° or 225° (Fig. 2, contralateral and ipsilateral columns), but it fired when the two arms moved in parallel towards 225° (Fig. 2b). It was less active in one other kind of bimanual trial (Fig. 2c) and failed to respond in the rest (Fig. 2a, d).

The neuron in Fig. 3A is from right MI, and fires before movements of the contralateral arm towards 45° (Fig. 3Aa, contralateral column). However, both arms together evoked a different pattern of activity (Fig. 3Aa, bimanual column). The late bimanual-related activity was almost completely absent when the monkey performed similar unimanual movements.

Many cells exhibited bimanual-related activity: 69% (53 of 72 in monkey F and 27 of 44 in monkey G) in MI and 64% (47 of 73) in SMA. This indicates that bimanual-related activity is at least as common in MI as in SMA. Note that these cells outnumber 'directionally selective' cells, suggesting that even classically 'unresponsive' neurons may participate in bimanual coordination. Table 2 shows the significance of many bimanual-related components, even by extremely strict criteria. The components in Figs 2

Table 1 Responsiveness and arm preference of MI and SMA cells in unimanual movements.

<table>
<thead>
<tr>
<th>Area</th>
<th>Total</th>
<th>Selective</th>
<th>Contra</th>
<th>Both (C &gt; I)</th>
<th>Both (I &gt; C)</th>
<th>Ipsil</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>MI (F)</td>
<td>72</td>
<td>50 (69%)</td>
<td>28 (62%)</td>
<td>13 (26%)</td>
<td>1 (2%)</td>
<td>10 (20%)</td>
<td>50 (100%)</td>
</tr>
<tr>
<td>MI (G)</td>
<td>44</td>
<td>22 (50%)</td>
<td>10 (45%)</td>
<td>4 (18%)</td>
<td>3 (13%)</td>
<td>5 (22%)</td>
<td>22 (100%)</td>
</tr>
<tr>
<td>SMA (F)</td>
<td>73</td>
<td>43 (59%)</td>
<td>14 (32%)</td>
<td>8 (19%)</td>
<td>6 (14%)</td>
<td>15 (35%)</td>
<td>43 (100%)</td>
</tr>
</tbody>
</table>

Neurons that responded in relation to both ipsilateral and contralateral arm movements were divided into two groups: those showing stronger modulations in relation to the contralateral arm (C > I), and those showing stronger modulations in relation to the ipsilateral arm (I > C).

Figure 1 Behavioural paradigm and task. A, The monkey sits in a primate chair holding two manipulanda and facing a video screen. Two cursors (+) indicate the location of the manipulanda. Each cursor appears in the corresponding origin. All target locations are shown as grey circles surrounding each origin. Ba–d, Examples of the four main types of trials (the open circles are not visible to the monkey). In the examples shown the selected direction was 135°. The monkey performed these four types along with complementary four types of movement in the opposite direction (315°).

Figure 2 SMA cell with bimanual-related activity. a–d, Each row contains peristimulus time histograms (PSTHs) and raster displays depicting the cell activity in one type of trial. The direction of movement of each arm is indicated above the graph by arrows or a black circle if the arm does not move. The cell had strong activation only during bimanual movements (b, left column) and no activity in unimanual trials (right column is unimanual right; middle column is unimanual left). Trials are aligned on the beginning of the movement (of the first arm) and sorted by reaction time. The target onset is indicated by circles. The number of trials (n = 127) and the PSTH scale are identical in all plots. The movement directions were 45° (−−) and 225° (−→).
and 3A are significant at a level of $P < 10^{-15}$. The cell in Fig. 3B demonstrates a weak bimanual-related component at the limit of statistical significance ($10^{-7}$) recorded in the left MI. Examination of the strength (Table 2), latency and duration of bimanual-related components in the two areas failed to reveal substantive differences in the character of bimanual-related activity in MI and SMA.

Observation of the monkeys during task performance did not reveal postural adjustments that distinguished movements during bimanual and unimanual trials. Visual inspection of the recorded trajectories, velocity profiles and electromyogram (EMG) showed that bimanual and unimanual movements were similar in many trials, although there were differences. For example, an analysis of EMG patterns similar to the one performed on the neural activity revealed that 24% of the patterns showed statistically significant differences (as opposed to 69% of the neurons). The large number of trials in each condition allowed an analysis of the relation between kinematics and cell activity. Figure 4 depicts the activity of one bimanual-related MI neuron. Trials in which unimanual and bimanual movements were similar are shown in the top displays; trials in which the movements were not similar are shown underneath. Figure 4 shows that selection of trials with similar trajectories in unimanual and bimanual conditions did not lessen the bimanual-related effect, and selection of trials with different trajectories did not increase it. Moreover, the temporal pattern of the neuron's activity is unaffected by the selection of trials. An analysis of variance (ANOVA) performed on the activity of the cell thus separated showed a highly significant difference between 'unimanual left' and 'bimanual parallel' ($P < 0.001$), and no significant effect of either the selection of trials by movement path (comparing Fig. 4a and b) or the interaction between the variables.

We performed similar analyses on velocity profiles and EMG. For the EMG, we analysed only the four muscles recorded simultaneously with neurons. For each of the three movement variables, we performed this analysis on 16 bimanually related neurons. In no case did the ANOVA indicate a significant effect on the bimanual-related activity, indicating that the bimanual components of many cells do not depend on precise kinematics or muscular activity.

Our results are in agreement with earlier studies in finding contralateral preference in MI, and also in finding significant, albeit weaker and less frequent, ipsilateral activation of MI. However, the discovery of bimanual-related activity in MI undermines the hypothesis that task-related activity in MI exclusively reflects movement of either limb alone. Indeed, the data suggest that information relevant to coordination effects neural activity of both MI and SMA.

We support the conclusions of previous work examining the bimanual-related activity of single neurons in MI and SMA, which found that a far greater proportion of units in the SMA respond to ipsilateral movements, and that a significant proportion of SMA neurons fire specifically in the bimanual task. We extend these findings to different types of bimanual movements, and demonstrate that neurons can be activated in relation to the specific nature of the bimanual coordination (Fig. 2).

One striking difference exists between our data and the previous work. We find that bimanual-related responses occur at least as frequently in MI as in SMA, whereas the previous work found that a very small fraction (2%) of MI neurons responded exclusively to the unimanual or exclusively to the bimanual movements. This difference may lie in the fact that our monkeys used their entire arm.
Table 2 Many cells in MI and SMA have highly significant bimanual-related components

<table>
<thead>
<tr>
<th>Significance level</th>
<th>MI for monkey F</th>
<th>MI for monkey G</th>
<th>SMA for monkey F</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;10^{-6}</td>
<td>13 (18%)</td>
<td>12 (27%)</td>
<td>15 (21%)</td>
</tr>
<tr>
<td>&lt;10^{-5}</td>
<td>22 (31%)</td>
<td>13 (30%)</td>
<td>20 (27%)</td>
</tr>
<tr>
<td>&lt;10^{-4}</td>
<td>33 (46%)</td>
<td>20 (45%)</td>
<td>32 (44%)</td>
</tr>
<tr>
<td>&lt;10^{-3}</td>
<td>53 (74%)</td>
<td>27 (61%)</td>
<td>47 (64%)</td>
</tr>
<tr>
<td>&lt;10^{-2}</td>
<td>60 (83%)</td>
<td>31 (70%)</td>
<td>53 (73%)</td>
</tr>
<tr>
<td>Total</td>
<td>72 (100%)</td>
<td>44 (100%)</td>
<td>73 (100%)</td>
</tr>
</tbody>
</table>

The cumulative number (cumulative percentage) of bimanual-related cells for which activity during bimanual movements differed significantly from activity during unimanual movements for different possible criteria of significance (for monkeys F and G). The level of significance used in the text is $P < 10^{-6}$.

Anatomic and lesion work has raised the suggestion\(^{16}\) that “each half of the brain has full control over arm, hand, and finger movements contralaterally but only controls arm movements ipsilaterally.” Similarly, studies on the callosal projections of MI have shown that the two hand representations are poorly connected, whereas the two arm areas are strongly connected\(^{14-17,20}\). It is possible that MI is wired contralaterally for distal movements and bilaterally for proximal ones, and that our findings are the electrophysiological correlate of this fact.

The differences we found may also be due to differences in muscle mechanics, if the cells that we recorded are primarily related to muscle activation\(^{11-12}\). However, it has been argued that cells in MI are more significantly related to the intended direction of movement than to precise muscle activation patterns\(^{21-25}\). Indeed, our results indicate that the bimanual-related components did not depend on the precise kinematics or muscle activation.

The most likely source of cortical representations of bimanual coordination are the callosal connections between the hemispheres. The importance of callosal connections for bimanual skills has been repeatedly demonstrated\(^{5,16}\), and perhaps temporal correlation between the hemispheres participates in generating the bimanual-related signal\(^{26-28}\). Whatever the source of the bimanual-related signal, our results imply that neuronal mechanisms modify the activity of both SMA and MI during bimanual movements. This mechanism might be the basis of interlimb coordination.

Methods

Animal and behavioural task. We used two female rhesus monkeys (Macaca mulatta) (4.5 and 4.2 kg). The animals’ care and surgical procedures used were in accordance with The NIH Guide for the Care and Use of Laboratory Animals (1996). A screen was located 30 cm from the monkey. Each trial began when the monkey centred both cursors on ‘origins’ (central circles: Fig. 1) and held them in place for 500 ms. For each arm, one of eight target circles (0.8 cm in diameter) appeared 3 cm from the origin. If only one target appeared (a unimanual trial) the monkey moved only the appropriate arm to achieve the target (Fig. 1a, b). If two targets appeared (a bimanual trial) the monkey moved both arms, achieving both targets simultaneously (Fig. 1c, d). Two classes of bimanual movements were tested in the recording sessions: parallel, and opposite, in which targets were separated by 180°. The level of significance used in the text is $P < 10^{-6}$.

Recording sessions. Recording chambers (27 × 27 cm) were implanted above both the right and left hemispheres under general anaesthesia in aseptic conditions. During recordings, the monkey sat in a primate chair in a dark chamber, and four electrodes were introduced into each hemisphere. The electrode signals were amplified, filtered and sorted (MCP-8000, MSD, Alpha-Omega), and all spike shapes were sampled at 24 kHz for off-line confirmation of spike sorting. We began data collection by testing the units ‘preferred’ directions for unimanual movements of each limb\(^{29}\). We collected data during performance of bimanual and unimanual movements in two directions separated by 180°, chosen on the basis of the preferred directions of selected units. At the end of each session, we examined the activity of neurons evoked by passive manipulation of the limbs. Finally, we applied intracortical microstimulation (ICMS; 500 ms of 200-μs cathodal pulses at 300 Hz with an intensity of 10–80 μA) to evoke movements.

Recording sites. We followed standard histological procedures to construct surface maps of all penetrations and to support the physiological definition of MI and SMA. The identification of the proximal arm areas of SMA and MI was based on neuronal responses during the task, passive limb movements, the effect of microstimulation, and the histological analysis. No attempt was made to record from the pre-SMA\(^{30}\). In MI we recorded almost exclusively on the bank, not in the depths of the central sulcus. In SMA we recorded almost exclusively on the medial wall.

Data analysis. We selected single neurons for analysis on the basis of our ability to isolate their spikes. Standard raster displays and peristimulus time histograms were examined. We considered cells to be directionally selective during unimanual movements if their activity before and during movement in opposing directions differed significantly. For example, in Fig. 3a, the contralateral activity in a was compared with that in b, demonstrating directional selectivity during contralateral movements. The Mann–Whitney rank statistic, calculated on the trial-by-trial firing rates during an interval of 500 ms starting 250 ms before movement initiation, determined the statistical significance of differences in activity. Repeating the analysis on a 250-ms epoch and a 1-s epoch did not affect our results. The level of significance used here is $P < 0.001$ for all statistical tests. We compared activity during bimanual movements with the corresponding unimanual movement to which the cell responded most strongly. Thus, four Mann–Whitney tests (one for each type of bimanual movement) were performed for each cell. For example, in Fig. 3aA we compared the bimanual and contralateral responses, and in Fig. 3Ab we compared the bimanual and ipsilateral responses. The significance over the four tests, and the criterion was divided by four to correct for the compounded tests. Our definition of bimanual-related activity is similar to the exclusive cells in previous studies of bimanual activity\(^{13,14}\). Our use of the term bimanual-related does not include cells with pronounced activity during both bimanual and unimanual movements (bilateral cells in previous studies).

EMG recording. We recorded surface EMGs for nine muscles bilaterally, including deltoid, rhomboids, pectoralis major, latissimus dorsi, teres major, biceps brachi, triceps brachii, flexor carpi ulnaris and extensor carpi ulnaris. We recorded two of these muscles (deltoid and flexor carpi ulnaris) bilaterally during neural recording sessions in monkey G.
Correspondence and requests for materials should be addressed to E.V. (e-mail: eilon@hbf.huji.ac.il).

Do blind persons develop capacities of their remaining senses that exceed those of sighted individuals? Besides anecdotal suggestions, two views based on experimental studies have been advanced. The first proposes that blind individuals should be severely impaired, given that vision is essential to develop spatial concepts. The second suggests that compensation occurs through the remaining senses, allowing them to develop an accurate concept of space. Here we investigate how an ecologically critical cognitive function, namely three-dimensional spatial mapping, is carried out by early-blind individuals with or without residual vision. Subjects were tested under monocular and binaural conditions. We find that early-blind subjects can map the auditory environment with equal or better accuracy than sighted subjects. Furthermore, unlike sighted subjects, they can correctly localize sounds monaurally. Surprisingly, blind individuals with residual peripheral vision localized sounds less precisely than sighted or totally blind subjects, confirming that compensation varies according to the aetiology and extent of blindness. Our results resolve a long-standing controversy in that they provide behavioural evidence that totally blind individuals have better auditory ability than sighted subjects, enabling them to compensate for their loss of vision.

We examined how subjects with congenital deficits affecting the peripheral visual system (retina and optic nerve) localized sounds in space. Four groups were tested: totally blind subjects (n = 8); blind subjects with residual vision in the peripheral field (n = 3); normally sighted but blindfolded controls (n = 7); and sighted controls (n = 29). Subjects were asked to localize a sound source presented on the horizontal plane. The sounds were delivered randomly through 16 loudspeakers mounted on a semicircular perimeter. Peri-central field was defined arbitrarily as the space covered by the four centrally located loudspeakers (up to 16° on either side of the midline), whereas the lateral fields extended to 78°. Subjects were tested under monaural and binaural conditions, each providing a specific set of cues to sound localization. Binaural cues refer to the discrepancies of inputs between the ears in terms of timing and intensity, whereas monaural cues arise from the spectral filtering of sounds by the circvolution of the pinna.

The sound-localization performance in the binaural condition is plotted in Fig. 1. Because a preliminary analysis showed that the mean error scores in each field were not different for blindfolded and sighted controls (P > 0.05), their results were pooled (Fig. 1a). The principal results indicate that totally blind subjects were at least

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**Early-blind human subjects localize sound sources better than sighted subjects**

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