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Rhesus monkeys employ a procedural strategy to reduce working memory load in a self-ordered spatial search task

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Abstract

Several nonhuman primate species have been reported to employ a distance-minimizing, traveling salesman-like, strategy during foraging as well as in experimental spatial search tasks involving lesser amounts of locomotion. Spatial sequencing may optimize performance by reducing reference or episodic memory loads, locomotor costs, competition or other demands. A computerized self-ordered spatial search (SOSS) memory task has been adapted from a human neuropsychological testing battery (CANTAB, Cambridge Cognition, Ltd) for use in monkeys. Accurate completion of a trial requires sequential responses to colored boxes in two or more spatial locations without repetition of a previous location. Marmosets have been reported to employ a circling pattern of search, suggesting spontaneous adoption of a strategy to reduce working memory load. In this study the SOSS performance of rhesus monkeys was assessed to determine if the use of a distance-minimizing search path enhances accuracy. A novel strategy score, independent of the trial difficulty and arrangement of boxes, has been devised. Analysis of the performance of 21 monkeys trained on SOSS over two years shows that a distance-minimizing search strategy is associated with improved accuracy. This effect is observed within individuals as they improve over many cumulative sessions of training on the task and across individuals at any given level of training. Erroneous trials were associated with a failure to deploy the strategy. It is concluded that the effect of utilizing the strategy on this locomotion-free, laboratory task is to enhance accuracy by reducing demands on spatial working memory resources.

1. Introduction

Foraging nonhuman primates (NHPs) may travel a circumscribed territorial range from day to day or from season to season in the search for food. Various food items occur in spatial groupings such as fruit or nut trees, termite mounds, edible leaf trees/bushes, etc. Search efforts may be optimized by remembering the location of such food sources for either a return visit (if not previously depleted) or avoidance (if recently exhausted). A paper by Altmann proposed (in his “Principle Nine” subsection) that foraging primates are best served by minimizing the travel distance per available calorie of food [1], thereby anticipating a subsequent literature on efficient search strategies. This body of work suggests

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the possibility that many nonhuman primate species optimize spatial routes based on a variety of representation regardless of whether the “map” depends on longer term reference memory (location of fruit trees in range), episodic memories (foraging visits in past days to weeks) or even shorter term, rapidly updating spatial working memory functions (as in lab-based experimental tasks). The field/foraging literature provides an intuitive motivation for search optimization based on reducing locomotor costs and/or the demands placed on episodic or reference memories [2–6]. In experimental studies the locomotor cost is lower, however animals are frequently motivated by appetitive payoff differences which attend more or less accurate response patterns. Several nonhuman primate species have shown evidence of spatial sequencing in artificial foraging-like spatial search tasks [7–10].

As reviewed by Janson and Byrne [11], most of prior work NHP spatial search behavior has been conducted with an ecological or comparative cognition approach. That is, simply describing how and if a given species forages, or performs experimental search tasks, in a manner consistent with non-random behavior that is most parsimoniously attributed to memory and/or planning. This literature distinguishes efficient search for *unknown* targets from the putative efficient sequencing of multiple *known* target locations; the present work is contextually related mostly to the latter. These approaches are less able to answer several essential questions. How optimal are the spatial search solutions? Are such solutions innate or do they develop with practice? A goal of the present study was to determine if analogous spatial “search paths” are used by monkeys performing a food-reinforced operant task to enhance their accuracy (e.g., maximizing the number of food pellets earned) even when long distance locomotion is not required. The present study investigates whether rhesus monkeys adopt efficient sequencing strategies in an experimental response task which depends on short-term, labile memory that is consistent with constructs of spatial working memory.

A nonverbal test designed primarily to assess spatial working memory has been developed for use in a computerized, nonverbal neuropsychological testing battery [12–14] applicable to human and nonhuman subjects. The self-ordered spatial search (SOSS) test (termed the “spatial working memory” test in some publications) was designed to be analogous to the radial arm maze frequently used in rodent studies and is reminiscent of the Hamilton search task [15]. The SOSS task requires the subject to make sequential responses to two or more targets (“boxes”) presented on a touch-sensitive computer display without repeating a previous response (Figure 1). Evidence suggests that this task depends essentially on frontal cortical structures in humans, since individuals with stroke-related damage to frontal cortex are impaired relative to those with temporal damage or normal control subjects [16]. The nonverbal nature of the SOSS task facilitated adaptation to nonhuman primates and studies in marmoset monkeys (*Callithrix jacchus*) confirmed the importance of frontal cortex since excitotoxic lesions of lateral and orbital prefrontal cortex impair performance on this task [17]. In addition, aged rhesus monkeys (*Macaca mulatta*) acquire the task more slowly than adult animals [18] and the performance of young adult rhesus monkeys is impaired in a dose- and trial difficulty-dependent manner by the amnestic drugs scopolamine [19] and ketamine [20]. Furthermore, performance of the SOSS task declines following infection with simian immunodeficiency virus on the macaque model of neurological Acquired Immune Deficiency Syndrome [21]. Thus the SOSS task is sensitive to a number of conditions reported to affect mnemonic function in monkeys.

Collins and colleagues (1998) have reported that marmosets tend to complete the task by responding to individual boxes within a trial in such a way as to describe an approximately circular path around the screen rather than describing an approximation of a line. To this pattern was also attributed a tendency to move from one box to the nearest adjacent one, thus minimizing the distance traveled (termed the “proximity” strategy). In contrast, rhesus monkeys which are well trained on the SOSS task have been observed anecdotally to

employ a noncircular, linear response pattern by initiating the trial at one corner of the screen and responding to boxes along a path toward the opposite corner of the screen. This performance difference may reflect a real species differences in strategy utilization or be a result of the extensive training history with randomized box locations that have been used for the rhesus monkeys [22]. In any case, if highly experienced rhesus monkeys consistently employ any strategy in the completion of the SOSS task it would suggest that they spontaneously (i.e., there is no explicit demand of the task that animals make sequential choices in any particular order) develop a procedural strategy to reduce the burden on working memory, potentially improving accuracy on the task. The main hypothesis under investigation in this study is a prediction that a distance-minimizing sequential response pattern within trials is associated with increased trial completion accuracy.

The report of Collins and colleagues raised a number of interesting methodological questions specific to this task. First, the position of the boxes was fixed for a set of trials employed for most of that prior study. Thus it is possible that the correspondence of the circling and proximity strategies was a unique outcome of the trial configuration. Given that this task has been used for testing 2–3 times per week for years in our studies, one of the necessary methodological goals was to create a strategy measure that was comparable across the randomly-determined trial types (Figure 2). Second, the authors failed to describe more than anecdotally the extent to which the proximity strategy was followed, reporting proximity strategy values as “60 to 70% of minimum possible scores”. Thus another important methodological goal was to quantify the optimization of monkey performance against all possible response patterns within each trial. Third, there was little attempt in that prior study to determine if differences in strategy utilization were associated with trial completion accuracy. As noted above, the primary hypothesis to be tested in the present study is that increased use of a distance-minimizing, TSP type solution to the SOSS task is associated with increased success on the task.

2. Results

2.1 Trial Completion Accuracy

Male rhesus monkeys (N=21) were trained in the Self-Ordered Spatial Search (SOSS) task (Figure 1) over a period of 24 months. Trial completion accuracy depended on the trial difficulty (3-box vs 4-box trial types) and improved steadily with repeated practice (Figure 3) as we have shown before [22]; training data for six animals in the present study were included in the first 16 mo of SOSS data in that prior report. Randomized block analysis of variance confirmed main effects of trial difficulty ($F_{1,20} = 259.5$; $p < 0.0001$), months of training ($F_{23,460} = 13.04$; $p < 0.0001$) and the interaction of both factors ($F_{23,460} = 2.46$; $p < 0.0001$). The Tukey-Kramer post-hoc test further confirmed that significantly more trials were completed successfully relative to the first two months for both 3-box (months 4–24) and 4-box (months 9–24) trial types.

2.2 Use of the Proximity Strategy

A similar steadily improving pattern was also observed for the use of a distance-minimizing proximity strategy which was created to be independent of specific trial configuration (Figure 2). Across two years of training the monkeys became increasingly likely to select trials in a sequence that minimized the distance “traveled” between each sequential response (Figure 3). Randomized block analysis of variance confirmed main effects of months of training ($F_{23,460} = 6.63$; $p < 0.0001$) and the interaction of both factors ($F_{23,460} = 2.43$; $p < 0.001$) but no significant effect of trial difficulty ($F_{1,20} = 1.09$; $p > 0.05$). The Tukey-Kramer post-hoc test confirmed that the strategy score was better relative to the first two months for both 3-box (months 20, 22, 24) and 4-box (months 13, 14, 16–24) trial types. To

give the range without detailing each of the possible comparisons, the post-hoc confirmed significantly better strategy scores for 4-box trials in months 21–22 relative to each of the first 9 months of training and in months 20–24 relative to month 8.

A similar strategy measure was calculated for those erroneous trials in which the error occurred on the final box choice. Unlike the strategy score for successfully completed trials, this measure was poor (~50% of the minimum possible distance) and did not change with repeated practice on the task. Randomized block analysis of variance confirmed main effects of trial difficulty ($F_{1,20} = 14.07$; $p < 0.005$) and the interaction of both factors ($F_{23,460} = 2.20$; $p < 0.005$) but no significant effect of months of practice ($F_{23,460} = 1.28$; $p > 0.05$). The post-hoc test did not confirm any differences relative to the first month within either trial difficulty type, nor between trial types at any month of practice.

2.3 Correlation of Accuracy with the Proximity Strategy

The individual correlations between trial accuracy and the strategy measure are depicted in Figure 4. Points depict monthly averages for individual animals. The correlations for the group means for all 24 months of training/testing are also presented. A negative correlation was observed in the group mean data and can also be observed in the individual differences. Months 1, 6, 12, 18 and 24 were selected for analysis purposes. Significant negative correlations were confirmed between accuracy and strategy (Table 1) for months 6, 12, 18 and 24. No consistent association was observed between accuracy and the error-strategy (calculated from trials on which the final response was erroneous).

3. Discussion

The present results show that rhesus monkeys employ a distance-minimizing response pattern in performing the self-ordered spatial search (SOSS) task of the Cambridge Neuropsychological Test Automated Battery (CANTAB). The success in employing such a search strategy is associated with increased trial-completion accuracy in two ways. First, monkeys as a group tend to refine and improve their use of the proximity strategy as their trial completion accuracy improves with practice. Second, individual differences in deploying the proximity strategy within a given level of training experience predict individual differences in accuracy. Finally, with protracted training, some individuals perform the SOSS task by selecting the very shortest, or next-shortest, proximity solutions on the majority of successful trials (i.e., ~20% strategy score, see Figure 3). This latter observation suggests that at least some rhesus monkeys are capable of calculating *ideal* traveling salesman-like solutions to the SOSS task on a consistent basis.

The proximity strategy emerged spontaneously in the monkeys under study. There is no requirement or incremental shaping in the task which would demand that monkeys adopt any particular pattern of sequencing their responses, only that they adhere to the rule to respond to each box location within a trial once and only once. Nor is it the case that the trial types presented here tax rhesus monkeys' capabilities to the limit; we have shown that they can perform up to 6-box and even 8-box trials [23, 24]. Thus these data support an inference that the strategy emerges because it leads to more successful performance. If raw short term spatial working memory is conceptualized as the ability to maintain the recent response status of several locations simultaneously, that would appear insufficient for best performance on this task. The use of a proximity strategy, or any sequencing strategy, could be viewed as reducing the demands on short term spatial working memory.

The individual differences in strategy utilizations, and the corresponding differences in trial completion success, may be important for further understanding certain health conditions under which memory fails. For example, Alzheimer's patients are impaired on a pen-and-

paper traveling salesman problem which does not require memory [25], suggesting that they are less able to use strategies to reduce the burden on memory capacity. It could be that in early stages, or other putative memory disorders, the problem may be attributable in whole or in part to a failure of memory-saving strategies, rather than a failure solely attributable to declining short term memory function.

It is important to note that although technically it is possible for the proximity strategy score to closely reflect the physical travel of the monkey's hand, this is very unlikely due to the experimental apparatus. The cage fronts have four openings (arranged at the vertices of a square) and the monkeys tend to use more than one opening in accessing the full screen. On a qualitative basis, the animals tend to reach through a hole for a given response and then bring their hand back inside the cage during the 2 sec screen blank within the trial therefore it is not even the case that their preferred response hand maps out a travel path in miniature. This type of hand movement throughout the task further highlights the disconnect between the cognitive search path and the motor responses that are involved in translating that cognitive mapping into physical responses. The locomotor cost, if any, is disconnected from task completion accuracy in the SOSS, thus it is most likely that the driving motivation in adopting and refining the proximity strategy is the associated improvement of the trial completion accuracy (and therefore increased reward pellet delivery).

Interestingly the strategy scores did not differ significantly between the 3-box and 4-box trial difficulty levels. Although the present strategy score was designed to be independent of box configuration it is not inherently obvious that strategy scores for all difficulty levels would be identical. For example, humans rely more on a pre-search planned strategy as the memory demands of a spatial search problem are increased [26]. The present results suggest that even when trial completion success differs by 1.5 – 2 fold due to trial difficulty, the strategy scores are similar.

When the present results are placed in context with prior literature on spatial search or foraging in NHPs, the generalized nature of the behaviors are striking. Regardless of whether the “task” requires longer term episodic and/or reference memory [2–5], shorter term episodic / longer term working memory [7–10] or what is clearly short-term spatial working memory in the present operant study, the NHPs create efficient response paths based on information which is not available from their current view. These types of memory have all been shown to be imperfect, particularly as the load (duration of recall, number of items, degree of manipulation/updating) increases. Thus tasks involving these processes might all benefit from any cognitive strategies which reduce memory burden. The inference of a memory burden in the present SOSS task is a parsimonious explanation for the fact that trial completion success on this task consistently decreases as the number of items per trial increases in conditions of excellent [19, 23] or decreased appetitive motivation [27], improves with practice [22] and is near perfect for the easiest trial type. Motivational, perceptual or motor explanations for this pattern are not as convincing as the inference that increasing the numbers of items induces a memory cost.

A somewhat broader question relates to type of strategy that was tested in this study. Since the problem confronting the subject in the SOSS task shares some representational similarity with the TSP, it is hypothesized that TSP solutions (shortest possible path between points) are adopted in the service of reducing memory load. Nevertheless, there is a significant locomotor / energetic cost, opportunity cost and potentially a competitive cost [28], associated with suboptimal foraging in the wild setting. Costs in the SOSS task are essentially limited to the opportunity cost of failing to get a trial correct. Thus it could be the case that the use of spatial sequence planning in this short-term working memory intense operant task is only an epiphenomenon of acquired cognitive properties of the primate brain.

The present data, which show a continued efficiency in deploying optimal search strategies across months of repeated training, suggest rather that this type of sequencing behavior is incrementally reinforced by the associated improvement in what is otherwise memory related trial completion success.

In summary, we have shown that rhesus monkeys performing the CANTAB Self-Ordered Spatial Search task of spatial working memory develop a nonmnemonic strategy which is refined or improved with protracted task experience. The strategy was to adopt a distance-minimizing search “path” that is akin to a traveling salesman problem solution, despite the fact that physical locomotion is not required in this task. The strategy measure is correlated with task accuracy as both a matter of individual differences and in terms of group effects over many months of training. It is inferred that this task is useful as a model of higher level strategic cognition which is deployed to reduce reliance on raw memory for multiple items under changing demand or identity conditions.

4. Experimental Procedure

4.1. Subjects

A group of 21 young male rhesus monkeys (*Macacca mulatta*) participated in the study. The monkeys were all 2–3 years of age and weighed 2.5–4 kg at the beginning of the study. Animals were individually housed and fed in the home cage after completion of the daily testing session. The animals' normal diet (Lab Diet 5038, PMI Nutrition International) was supplemented with fruit or vegetables four days per week and water was available *ad libitum* in the home cage. Individual feeding restriction levels 5 days per week (Sun-Thur) were determined by practices established over the years of development of this model with the goal of maintaining consistent behavioral performance. Under such protocols developing animals gain weight at an average rate of 0.06 kg/month prior to puberty and 0.14 kg/month thereafter with a distribution substantially overlapping that reported for a group of well provisioned free ranging macaques [29]. Principles of laboratory animal care [30] were followed, and all protocols were approved by the Institutional Animal Care and Use Committee of The Scripps Research Institute.

4.2. Behavioral Testing

4.2.1 Apparatus—For behavioral testing, animals were transferred to transport cages similar to the home cage but modified by the removal of several bars from the front of the cage to allow the animal to easily reach out. The transport cage was placed in front of a touch-sensitive computer monitor on which the stimuli were presented. All animals had been previously trained to reach out of the cage to touch the location on the screen at which visual stimuli were presented to obtain a food pellet reward. Stimulus presentation and response detection were controlled by a micro-computer equipped with a version of the Cambridge Neuropsychological Test Automated Battery (CANTAB; Cambridge Cognition, Ltd., Cambridge, UK) designed for use with non-human primates. A dispenser delivered 190 mg flavored pellets (Noyes Precision Pellets; Research Diets, Inc., New Brunswick, N.J.) to a bin mounted on the front of the cage after correct responses were made. Initial training of the monkeys employed two slightly different strategies as has been previously outlined [22].

4.2.2. Self-Ordered Spatial Search task—In each trial of the SOSS task small colored rectangles (boxes) are displayed on the screen in positions randomly allocated from 16 possible locations (see Figure 1 for schematic). A trial would typically present two, three or four boxes although up to 16 boxes are possible. The animal was required to touch a box within 30 seconds of stimulus onset. After each successful touch, the color of the touched box was briefly (100 ms) changed and then the screen was blanked and a reinforcer is

delivered. After a 2 second delay, the boxes were re-displayed and the animal was required to touch a box which had not previously been touched in the trial. The trial was completed when the animal had either touched all boxes without a repetition (correct), touched a box that had previously been selected in that trial (error) or failed to touch a box within 30 seconds of stimulus presentation (omission). Errors and omissions were followed by a tone and a 4 second screen blank. After an inter-trial interval of 5 seconds, another trial was presented with stimuli in new (randomly allocated) positions. A typical session consisted of 40 trials grouped into 6 blocks by trial type as follows: 5 (2 boxes), 7 (3 boxes), 7 (4 boxes), 8 (3 boxes), 8 (4 boxes), 5 (2 boxes). Accuracy scores were calculated for each trial type by dividing the number of correctly completed trials by the number of trials in which there was at least one response (i.e., errors of omission are excluded from the calculation).

4.2.3. Training—The SOSS task was the first major task trained in a multi-task battery of cognitive and behavioral tests, as has been described [21]. Animals were therefore performing the SOSS task ~ 5 days per week in the first six months of training and then reduced to 2–3 days per week on the task as additional complex tests were added to their repertoire over time. All baseline training sessions run in a given month were averaged within individual to provide the unit of data analysis for this study. No data are included from animals following manipulations intended to test permanent or lasting effects. No data are included from acute challenge sessions prior to which drugs were administered.

4.2.4. Calculation of the "proximity" strategy score—A measure of search strategy (for trials consisting of more than 2 boxes) was derived from the self-selected order of responses on each correct trial. To calculate the strategy score, the distance (in screen pixels) between each sequential box selection was summed for each successfully completed trial. This distance was then represented as a proportion of the difference between the minimum and maximum possible routes for a given trial (Figure 2). Therefore, a strategy score approaching 0% represented an animal consistently choosing to respond sequentially to the next-closest box, whereas a strategy score approaching 100% represented consistently choosing the most-distant box from the previous choice (the extremities of the distribution required starting at a location that varied by trial). This novel analysis of search strategy in this task is similar to the "proximity strategy" described by Collins and colleagues [17] but has the advantage of providing comparable scores independent of either the number of boxes per trial or the location of the boxes in a given trial. In that prior study, marmosets were presented with sessions in which the box locations in each trial were scripted for the entire session, thus each animal always completed the same trials as the rest of the subjects. For the present study, the trials were always randomized meaning that box locations vary between and within animals from session to session. As is illustrated in Figure 2 for a sample of eight 4-box trials, the path lengths for all possible path permutations (4 factorial = 24) might range from 425 (Trial 7) to 1267 (Trial 4) pixels, and the range of possible different path lengths within a trial might range from 246 (Trial 6) to 666 (Trial 4) pixels. Thus it was necessary to develop a relative measure so that strategies might be compared between trials on which the box locations (and therefore the total path) differed.

A strategy score for error trials in which the subject commits the erroneous response (repeats a box) on the last response of the trial may also be calculated with this approach. This is because if the monkey touched N-1 boxes without an error, the necessary sequence for a correct outcome had been established. Thus if the strategy on such error trials tended to be identical to the strategy employed on correctly completed trials it would suggest that errors are mostly due to forgetting the location of the previous responses. On the other hand, a higher error-strategy score would suggest that errors are due to incorrect employment of the strategy on those particular trials, i.e. a poor choice of start box or a misapplication of the strategy. *N.b.* This measure was undefined for 7 individuals in the first 12 months of training

for the 3-box trials and for 5 individuals in the first 4 months for 4-box trials because insufficient numbers of qualifying errors were made.

4.3. Data Analysis

Analysis of the SOSS data (percent correct trials, strategy score, error strategy score) employed analysis of variance (ANOVA) with within-subjects factors of trial difficulty (3-boxes, 4-boxes) and months of training. Simple correlations (Pearson r) were used to compare a relationship between percent correct trials and the proximity strategy and error strategy measures for five monthly averages at 6 month intervals (1, 6, 12, 18 and 24 months). Post-hoc analyses of significant main effects in the ANOVA were conducted using the Tukey-Kramer test including all pairwise comparisons; the criterion for significance was $p < 0.05$. Analyses were conducted with GB-STATv7.0; Dynamic Microsystems, Silver Spring MD.

Highlights

- An examination of sequencing strategy in a spatial search task for monkeys
- Data show a distance-minimizing response “path” is associated with accuracy
- A traveling-salesman-like strategy emerges despite the lack of locomotor cost
- Monkeys use such strategies to decrease working memory load

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Figure 1.

The 16 possible locations in which boxes might be presented for the SOSS task are illustrated in the left panel. A response path dictated by a distance-minimizing search strategy is illustrated for a sample 4-box trial in the center panel. A suboptimal strategy which does not minimize the distance traveled is represented for the same trial in the right panel. Numbers indicate the sequence of responses and the open box highlights the starting position.

Search Path Permutations (4-Box Trials)

Proximity Strategy Score

Raw Path Length

Figure 2.

The proportional proximity strategy scores associated with each of 24 possible response sequences are presented for a sample of eight 4-box trials (upper panels). The corresponding raw path lengths in screen pixel units for the same eight trials are represented in the center and lower panels. Pairs of identical length search paths in upper and lower panels indicate the same path traveled in opposite directions.

Figure 3.

The mean ($N = 21$; $\pm$ SEM) accuracy, strategy for correct trials and error strategy scores are depicted across 24 months of training for 3-box and 4-box trials. Accuracy depends on trial difficulty whereas strategy scores do not. Accuracy and strategy for correct trials tend to improve with training duration whereas error strategy does not. Open symbols depict a significant difference from Months 1–2 and between difficulty conditions within a given month. Shaded symbols depict a significant difference compared with Months 1–2 only.

Individual Differences in Strategy Utilization

Figure 4. Individual ($N = 21$) accuracy scores are plotted against strategy scores for each of the initial 24 months of training. The achievement of higher average accuracy was associated with a lower average proximity score. Individuals differed substantially in terms of both accuracy and strategy utilization.

Table 1
Correlation between Accuracy and Strategy

Correlations between the percent correct trials and strategy, between the percent correct trials and strategy for trials in which the final response was erroneous and between strategy for correct and final-response-erroneous trials are presented. With training, a negative correlation between accuracy and strategy on correct trials is observed. No other consistent associations were observed.

	Percent Correct Trials		Strategy
	Strategy	Error Strategy	Error Strategy
Month 1	r: -0.29	r: -0.11	r: 0.36
(N = 20)	r ² : 0.08	r ² : 0.01	r ² : 0.13
	p = 0.21	p = 0.64	p = 0.12
Month 6	r: -0.49	r: 0.38	r: -0.12
(N = 18)	r ² : 0.24	r ² : 0.14	r ² : 0.02
	p = 0.04	p = 0.12	p = 0.62
Month 12	r: -0.50	r: -0.43	r: 0.73
(N = 21)	r ² : 0.25	r ² : 0.18	r ² : 0.53
	p < 0.05	p < 0.05	p < 0.001
Month 18	r: -0.67	r: 0.50	r: 0.11
(N = 21)	r ² : 0.45	r ² : 0.25	r ² : 0.01
	p < 0.001	p < 0.05	p = 0.65
Month 24	r: -0.61	r: 0.28	r: 0.18
(N = 19)	r ² : 0.37	r ² : 0.08	r ² : 0.03
	p < 0.01	p = 0.23	p = 0.46