

## Prospective Processing: Behavioural and Neural Evidence

MICHAEL COLOMBO<sup>1)</sup>, AYLIN KLARER<sup>2)</sup>,  
MELISSA JOHNSTON<sup>1)</sup>, and JONAS ROSE<sup>3)</sup>

**Abstract** Whether animals can engage in prospective processing, looking ahead to what needs to be done, is an area of current interest in comparative cognition. We review some of the early behavioural and more recent neural evidence for prospective processing. Three classic behavioural studies, each adopting a different technique (confusion matrix design, sample-comparison mapping design, and modality-specific interference design), confirm that animals can engage in prospective processing. Mirroring these findings are more recent data that revealed neural evidence in favour of prospective processing. Overall, both behavioural and neural studies support the view that animals engage in prospective processing and plan for a future event.

**Key words** : prospective processing, delayed matching-to-sample, delayed paired-associate task, planning for the future

### 1. Introduction

What an animal remembers in a delay period between two events is a topic of considerable interest and impacts on many current themes in comparative cognition. The classic task used to assess memory across a variety of different animals is the delayed matching-to-sample (DMS) task. Take the case where an animal is trained on an identity DMS procedure with two stimuli, red and green. A session typically consists of a number of trials separated by an intertrial

interval. A trial proceeds as follows. At the end of the intertrial interval, either red or green is presented as a sample stimulus. After responding to the stimulus (e.g., pecking it in the case of a pigeon), the sample is turned off and a delay period ensues. At the end of the delay period, both red and green are presented as comparison stimuli, and to obtain a reward the animal must respond to the comparison stimulus that it saw most recently as a sample stimulus. On half of the trials red serves as the sample stimulus and on the other half of the trials green serves as the sample stimulus.

The question that has been the subject of a considerable number of studies is: *What are the animals remembering during the delay period?* If an animal is remembering the sample stimulus, then they are engaging in retrospective processing. On the other hand, if an animal is anticipating what to respond to when the comparison stimuli appear, then they are engaging in prospective processing. Naturally, it is difficult to determine whether an animal is engaging in retrospective or prospective processing with an identity DMS

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1) Department of Psychology, University of Otago, Dunedin, New Zealand

Department of Psychology University of Otago PO Box 56 Dunedin, 9054 New Zealand

2) Animal Physiology, Institute of Neurobiology, University of Tübingen, Tübingen, Germany  
Auf der Morgenstelle 28, University of Tübingen, 72076, Tübingen, Germany

3) Fakultät für Psychologie, Ruhr-Universität, Bochum, Germany  
Universitätsstr. 150, GA 04/47, 44801, Bochum, Germany

Corresponding author: MICHAEL COLOMBO  
E-mail: colombo@psy.otago.ac.nz

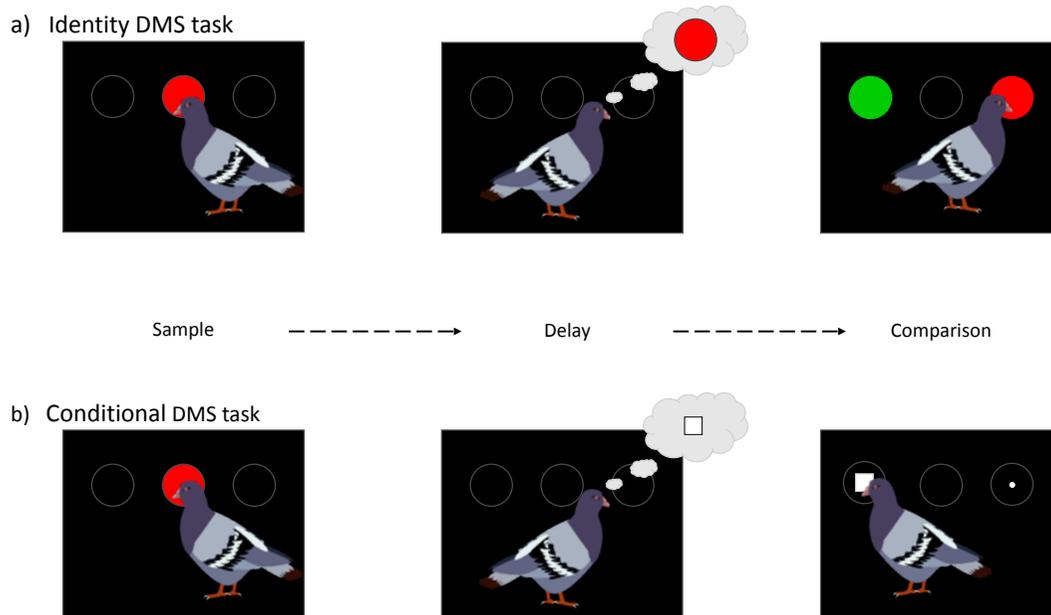
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task where the comparison stimuli are the same as the sample stimuli. Take the case, for example, where the sample stimulus is red (Figure 1a). If the animal engages in retrospective processing then it remembers “red” throughout the delay period. Similarly, if the animal engages in prospective processing and remembers the correct stimulus to respond to during the comparison phase, it is also remembering “red” throughout the delay period.

To determine whether an animal can engage in prospective processing, a conditional DMS task must be used in which the sample stimuli are mapped on to physically different comparison stimuli. Let’s take a conditional DMS task in which the sample stimuli, red and green, are mapped onto two different comparison stimuli, square and dot, such that when red is presented as the sample stimulus the correct response is to respond to the square comparison stimulus,

whereas when green is presented as the sample stimulus the correct response is to respond to the dot comparison stimulus. Again, take the case where the sample stimulus is “red” (Figure 1b). Under these conditions, if the animal is engaging in retrospective processing then it is remembering “red” throughout the delay period, whereas if it is engaging in prospective processing then it is remembering “square” throughout the delay period.

For some time the prevailing view was that animals remembered what they just saw, in other words, engaged in retrospective processing (Roberts, 1972; Roberts & Grant, 1976). *Is there any evidence that animals can engage in prospective processing?* The notion of prospective processing is interesting because it speaks to an ability to look ahead in time, to engage in mental time travel, something that nowadays is very topical in the field of animal cognition. But well before



**Figure 1.** DMS procedure. a) In an identity DMS task, if a pigeon is remembering, for example, red, it is unclear whether they are engaging in retrospective or prospective processing. b) In a conditional DMS task, the sample stimuli are physically different from the comparison stimuli so the stimulus remembered during the delay period can indicate whether the animal is engaging in retrospective or prospective processing. In the case of the example, the pigeon is remembering “square”, and hence engaging in prospective processing. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

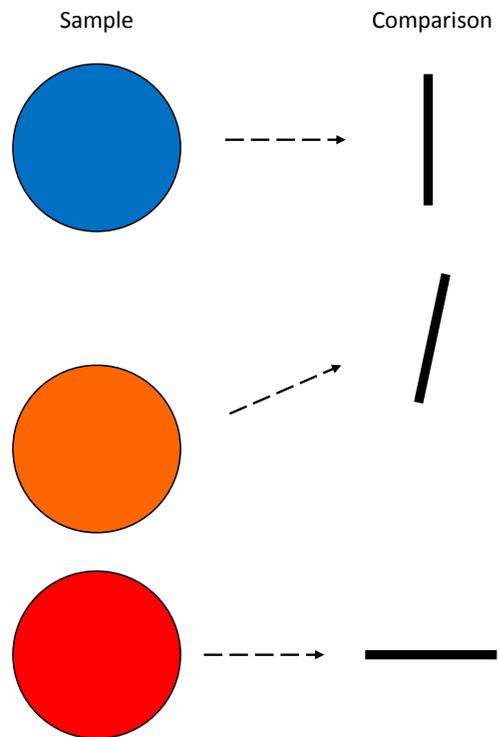
the notion of mental time travel and episodic memory, there were, in fact, a number of studies that indicated that animals could engage in prospective processing. In this review we will present some of the early evidence that animals could engage in prospective processing, and then examine more recent neural evidence for prospective processing.

## 2. Prospective Processing: Behavioural Studies

### 2.1 Confusion matrix design

Roitblat (1980) was one of the first to tackle the issue of whether animals can engage in prospective processing by using a clever confusion matrix design. The principle behind the confusion matrix design is that as a delay interval increases there should be more confusion between similar items than dissimilar items. Pigeons were trained on a conditional DMS task with three types of colour sample stimuli and three types of line tilt comparison stimuli (some birds received the reverse arrangement). The procedure was such that similar sample stimuli were mapped on to dissimilar comparison stimuli (Figure 2). Take, for example, the case of an animal trained with the three colour sample stimuli blue, orange, and red, and their corresponding three correct comparison stimuli (vertical line-0 degrees, tilted line-12.5 degrees, and horizontal line-90 degrees). On each trial the animal saw one sample stimulus, and then following a delay was presented with all three comparison stimuli. Note that in the confusion matrix design, the two similar sample stimuli (orange and red) are mapped onto two dissimilar sample stimuli (tilted line and horizontal line). Similarly, two similar comparison stimuli (vertical line and tilted line) are mapped onto two dissimilar sample stimuli (blue and orange).

By examining the types of errors that were made Roitblat (1980) was able to show that as the delay increased animals tended to confuse similar comparison stimuli rather than similar sample stimuli. Let's imagine the three possible trial types expressed as



**Figure 2.** Confusion matrix design. Either blue, orange, or red appear as the sample stimulus. At the end of a delay period, vertical, slant, and horizontal line are shown to the bird. Note that the two similar sample stimuli map onto two dissimilar comparison stimuli, and the two similar comparison stimuli map onto dissimilar sample stimuli. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the sample stimulus with the associated correct comparison response: blue-vertical, orange-tilted, and red-horizontal. If the animals were engaging in retrospective processing then they should perform poorly with orange-tilted and red-horizontal trial types because the sample stimuli orange and red are most easily confused. In contrast, if the animals were engaging in prospective processing they should perform poorly on blue-vertical and orange-tilted trial types, because the comparison stimuli vertical line and tilted line are most easily confused. Indeed, it was this latter condition that proved to be the case, thus suggesting that the pigeons were engaging in prospective

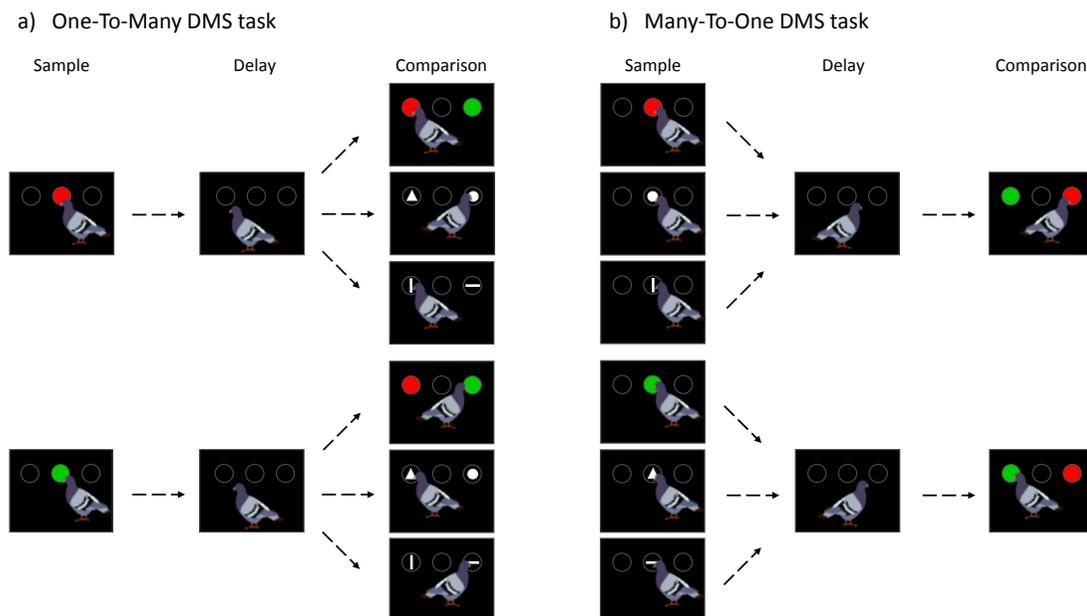
processing and converting the colour sample stimulus into the appropriate line orientation comparison stimulus, and remembering that information during the delay period.

## 2.2 Sample and comparison mapping design

Another technique used to reveal evidence for prospective processing in animals is sample/comparison mapping variation. Santi and Roberts (1985) trained animals on a conditional DMS task in which different numbers of sample stimuli were mapped onto different numbers of comparison stimuli. In the One-To-Many (OTM) condition, the animals were trained with two possible sample stimuli mapping onto six possible comparison stimuli (Figure 3a). Specifically, the animal could see either red or green as a sample stimulus, and after a delay period, the animal was presented with one of three different pairs of comparison stimuli (either red and green, or triangle and circle, or vertical line and horizontal line). If the

sample stimulus was red then the correct comparison stimulus to choose was, depending on which pair was shown, either red, circle, or vertical line. On the other hand, if the sample stimulus was green then the correct comparison stimulus to choose was, again depending on which pair was shown, either green, triangle, or horizontal line.

In contrast to the OTM condition, in the Many-To-One (MTO) condition the animals were trained with six possible sample stimuli mapping onto two comparison stimuli (Figure 3b). Specifically, the sample stimuli were red, circle, vertical line, green, triangle, or horizontal line (note on each trial only one sample stimulus was shown to the animal) and the same two stimuli, red and green, always appeared on every trial as the comparison stimuli. If either red, circle, or vertical line had appeared as the sample stimulus then the correct comparison stimulus to choose was red, whereas if green, triangle, or horizontal line had appeared as



**Figure 3.** Sample and comparison mapping design. a) In One-To-Many DMS, either red or green appear as a sample stimulus and then after the delay period the pigeon sees one of three possible pairs of stimuli, red and green, triangle and circle, or vertical line and horizontal line. b) In Many-To-One DMS, one of six stimuli can serve as the sample stimulus and the comparison stimuli always consist of red and green. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the sample stimulus, the correct comparison stimulus to choose was green.

The logic behind the experiment was as follows. If the animals were engaging in prospective processing then one would expect MTO performance to be better than OTM performance. *Why?* Take the case where an animal is presented with red as the sample stimulus. If the animal was prospectively processing in the MTO condition they would only need to remember the correct stimulus associated with red, namely red. On the other hand, if an animal was prospectively processing on the OTM task and red was the sample stimulus they would have to remember three stimuli (red, circle, and vertical line) because they would not know which of the three pairs of comparison stimuli was going to appear at the end of the delay period. Hence, if the animal was engaging in prospective processing, MTO performance should be better than OTM performance.

The case for what would provide evidence for retrospective processing is not as clear. The natural tendency might be to argue the opposite, that if an animal is retrospectively processing then OTM performance should be better than MTO performance. In actual fact, it is likely that if an animal were engaging in retrospective processing there would be no difference in performance between the OTM and MTO tasks. The reason is simple. Admittedly, MTO has six sample stimuli to draw from whereas OTM has only two, but the key fact is that irrespective of the number of sample stimuli in the possible pool, an animal only ever sees *one* sample stimulus, and hence retrospective processing in the MTO or OTM would only ever result in the animal remembering one sample stimulus. In fact, the data were clear, MTO performance was consistently better than OTM performance, an outcome only accommodated by the fact that the animals were engaging in prospective processing.

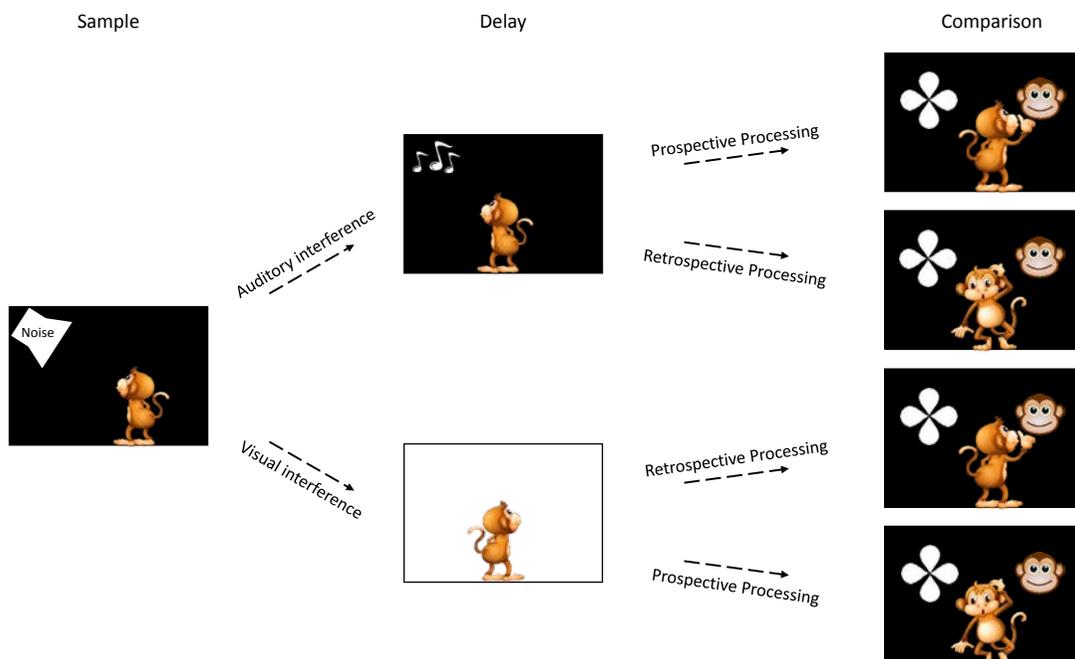
### 2.3 Modality-specific interference design

Colombo and Graziano (1994) tackled the

problem of prospective processing in a different manner to the previous studies by tapping into the notion of modality-specific interference, which refers to the fact that the best way to interfere with a memory is to require an animal to process information that is of the same modality as the to-be-remembered information. Thus in a visual DMS task, where the sample and comparison stimuli are all visual, the best way to disrupt the visual memory, be it either retrospective or prospective, is to encourage an animal to engage in visual processing during the delay period, typically by turning a light on during the delay (D'Amato, 1973). Filling the delay period with auditory stimulation has no effect on visual memory (D'Amato, 1973). In contrast, when monkeys are trained on an auditory DMS task with auditory sample stimuli and auditory comparison stimuli, the same visual interference that impaired visual DMS performance now has no effect on auditory DMS performance, and the same auditory interference that had no effect on visual DMS performance now does impair auditory DMS performance (Colombo & D'Amato, 1986).

Capitalizing on the notion of modality-specific interference, Colombo and Graziano (1994) trained monkeys on a conditional DMS task with two auditory sample stimuli (a high-frequency tone or a burst of white noise) and two visual comparison stimuli (a picture of a monkey face and a picture of four-lobed pattern) such that when the sample stimulus was noise the correct choice was to select the face comparison stimulus, whereas when the sample stimulus was the high-frequency tone, the correct choice was to select the four-lobed pattern comparison stimulus (Figure 4). The monkeys were free to solve the task in whatever manner they wished, by either retrospectively remembering the auditory sample stimulus throughout the delay period, or by prospectively remembering the correct visual comparison stimulus throughout the delay period.

To determine which processing strategy the monkeys adopted, Colombo and Graziano



**Figure 4.** Modality-specific interference design. The monkeys were trained on a conditional auditory-visual DMS task with auditory sample stimuli (high-frequency tone or a burst of noise) and visual comparison stimuli (4-lobed pattern and a picture of a monkey face). In the delay period the monkeys were presented with either auditory interference (music, top middle panel) or visual interference (lights on, bottom middle panel). If the monkeys were engaging in retrospective processing and remembering the sample stimulus then delay-interval music should impair performance and not delay-interval light. If the monkeys were engaging in prospective processing then delay-interval light should impair performance and not delay-interval music.

(1994) delivered either auditory or visual stimulation during the delay period and examined which form of stimulation affected performance. If delay-interval auditory stimulation affected performance then this would indicate that the monkey was remembering auditory information during the delay period and indicate a retrospective processing strategy. On the other hand, if delay-interval visual stimulation affected performance then the monkey must be remembering visual information throughout the delay period, and this would indicate a prospective processing strategy. Indeed, delay-interval visual stimulation affected performance, whereas delay-interval auditory stimuli had very little effect, suggesting that the animals were engaging in prospective processing. The animals were therefore hearing the auditory sample stimuli and converting the auditory samples into the

correct visual comparison stimuli that needed to be pressed, and remembering visual information throughout the delay period.

## 2.4 Summary

The aforementioned studies represent a small sampling of the studies that have examined the topic of prospective processing in animals. More recent instantiations of prospective processing studies have examined the evidence for episodic memory and mental time travel in animals (see Colombo and Hayne, 2010, for a full review of these studies). The evidence is overwhelming that animals have the capacity to engage in prospective processing. On this point, one final study deserves mention. Cook, Brown, and Riley (1985) trained rats on a 12-arm radial maze task and introduced a delay following either 2, 4, 6, 8 or 10 successful

arm entries. By charting the errors that the rats made, they found that rats adopted a strategy, either prospective or retrospective, that would result in them having to remember the least amount of information. And the switch from one strategy to the other occurred within a session and was a function of the current load on memory. Thus it is not necessarily the case that an animal will choose to engage in one strategy or the other on a particular task, but rather can switch between the strategies depending on the current memory demands.

### 3. Prospective Processing: Neural Studies

A number of studies have explored the neural basis of learning and memory across a variety of different animals and have reported neural evidence for their animals engaging in prospective processing. Different types of neural codes have been reported for the prospective processing of sensory information, as well as the prospective processing

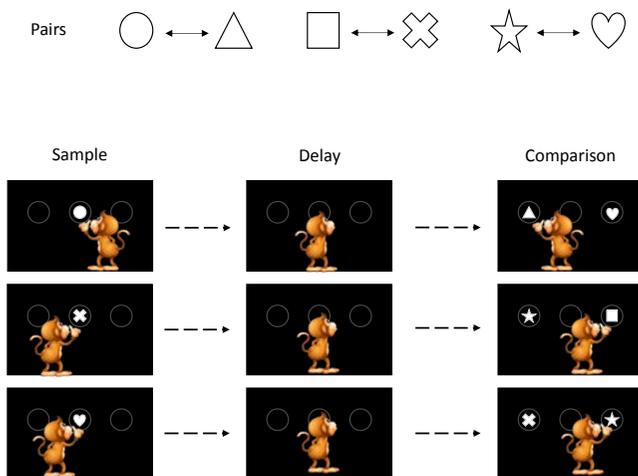
of reward information.

#### 3.1 Prospective processing of sensory information

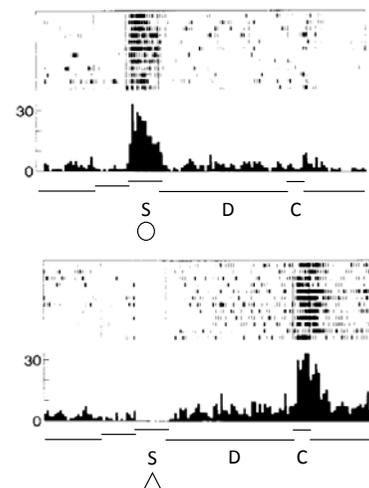
Sakai and Miyashita (1991) recorded from visual areas of monkeys trained on a pair-association task in which a sample stimulus was followed by a delay period and then the presentation of two comparison stimuli, of which one was the paired associate of the sample. Effectively, the pair-association task is very similar to a conditional DMS task, with the exception that in the pair-association task there are many more pairings, and either paired associate could serve as the sample stimulus (Figure 5a).

Sakai and Miyashita (1991) noted that one type of neuron, called a pair-recall neuron, exhibited a pattern of neural responses indicative of prospective processing. The first condition that a neuron must satisfy to be considered a pair-recall neuron is that it must show increased activity to one of the

a) Pair-Association task



b) Neural evidence

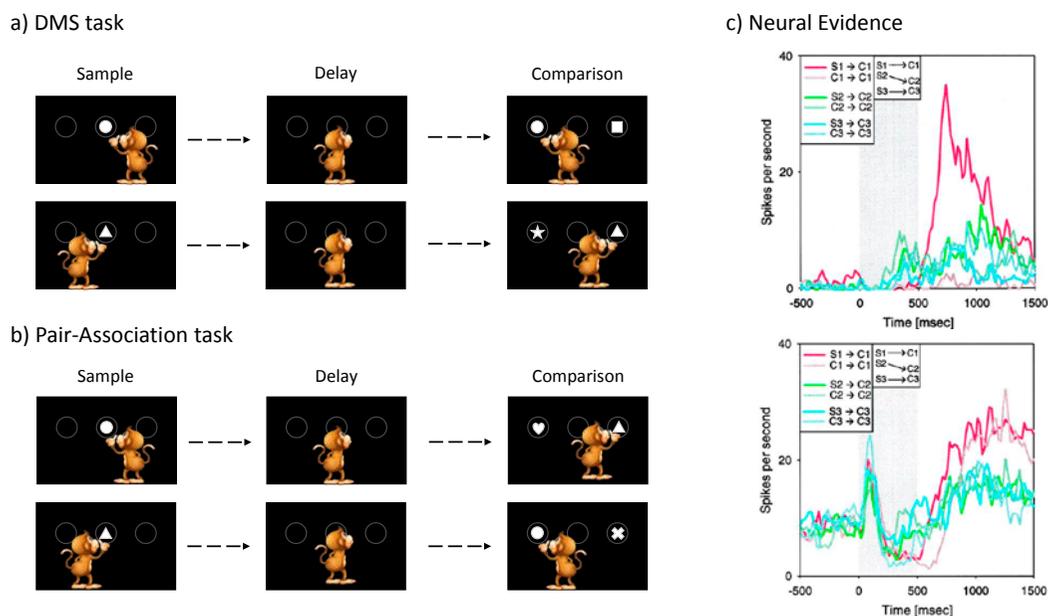


**Figure 5.** Sakai and Miyashita (1991) pair-association study. a) Monkeys were trained on a pair-association task in which one stimulus of a pair served as the sample stimulus, and following a delay period, the paired associate of that stimulus and another stimulus served as the comparison stimuli. The task required that the animal respond to the paired associate of the sample stimulus. b) Neural responses from a cell in inferior temporal cortex, a visual area of the primate brain. In the top panel the cell fires to a picture of the circle when it appears as the sample stimulus. In the bottom panel, the same cell fires in the delay period after the paired associate of circle (triangle) appears as the sample stimulus. The actual stimuli used in the study consisted of computer-generated flower-like patterns. The neural data are reprinted, with permission, from Sakai and Miyashita (1991).

two paired associates. Take the case where the neuron fires to circle and not to triangle (Figure 5b). In and of itself that reflects nothing more than a cell that has a preference for circle over triangle, a common occurrence in the visual areas of the brain. What makes this neuron a pair-recall neuron is that when triangle now served as the sample stimulus the cell would also show increased activation, not to triangle (because it doesn't fire to triangle) but during the delay period prior to when the animal would have received circle as one of the two comparison stimuli. In other words, the neural activity during the delay period represents a prospective code of the upcoming correct paired-associate stimulus.

Neural correlates of prospective processing have also been found in the prefrontal cortex (PFC). Rainer, Rao, and Miller (1999) trained

monkeys on a behavioural protocol consisting of alternating blocks of the DMS and pair-association tasks. Monkeys were first presented with a sample stimulus, and then after a delay, a target stimulus, to which the animals had to indicate whether it was a “match” or “nonmatch”. In the DMS task one of three stimuli (S1, S2, or S3) appeared as the sample, and one of the same three stimuli appeared as a comparison stimulus along with another comparison stimulus (Figure 6a). In the pair-association task the sample stimuli were either S1, S2, or S3, or their paired associates C1, C2, or C3 (Figure 6b). To determine whether the monkeys used retrospective or prospective processing, the authors applied Roitblat's (1980) “confusion matrix” design where two similar sample stimuli were associated with two dissimilar target stimuli, and two dissimilar sample



**Figure 6.** Rainer et al. (1999) prospective coding study. Monkeys were trained on both an a) identity DMS task as well as a b) pair-association task. c) Neural responses from cells in prefrontal cortex. In the insert are shown the pairing of the sample and comparison stimuli. In the top panel, the cell responds in the delay period after the S1 sample, a pattern of activity consistent with a retrospective code. In the bottom panel a different cell fires in the delay period (500-1500 ms) after either the S1 or C1 sample. Both S1 and C1 map into C1 as a comparison stimulus, and hence this is an example of a prospective memory cell. The actual stimuli used in the study consisted of multi-coloured images of real world objects. The neural data are reprinted, with permission, from Rainer et al. (1999). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

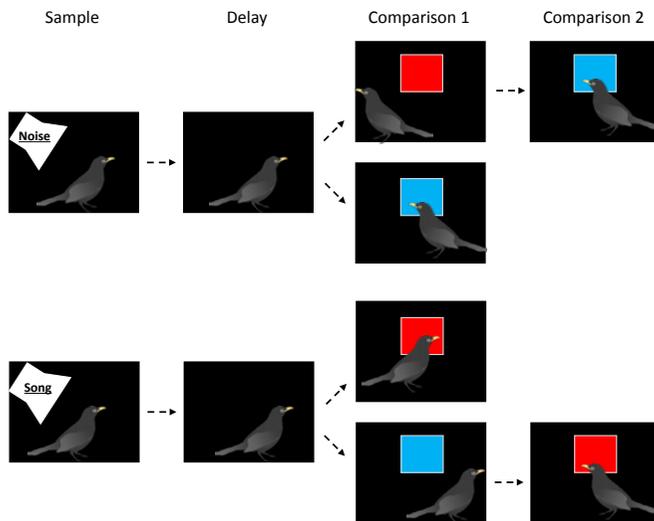
stimuli with two similar target stimuli. Indeed the patterns of errors suggested that Rainer et al.'s (1999) monkeys, much like Roitblat's (1980) pigeons, were engaging in prospective processing.

While the monkeys performed the DMS and pair-association tasks, Rainer et al. (1999) recorded neuronal activity in PFC. They found neurons that displayed evidence of both retrospective and prospective processing. Take the case of the cell in Figure 6c (top panel). This cell shows activation in the delay period (500-1500 ms) only when S1 served as the sample stimulus, an outcome consistent with the view that the delay activity represents a retrospective code of the sample stimulus. On the other hand, the cell in Figure 6c (bottom panel) shows a different

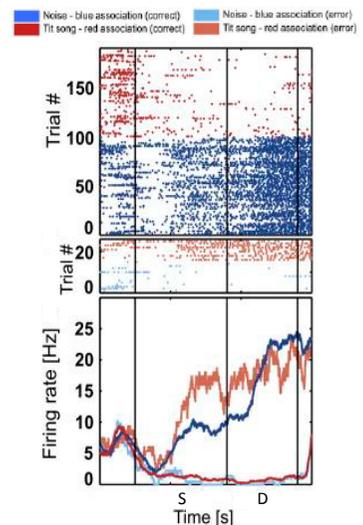
pattern of neural activity. For this cell, there is no difference in activity in the sample period to any of the six sample stimuli. On the other hand, in the delay period, this cell fires strongly if the sample stimulus was either S1 or C1. Since both S1 and C1 map onto C1, the pattern of neural activity is consistent with a prospective code.

Evidence for prospective processing has also been found in the neural processing of cells in birds in a structure known as nidopallium caudolaterale (NCL), the avian equivalent of the mammalian PFC (Güntürkün, 2005a, 2005b). Moll and Nieder (2015) trained two crows on an audio-visual conditional DMS task (Figure 7a) to select a blue square when the sample stimulus was a burst of noise, and the red square when the sample

a) A-V DMS task



b) Neural evidence



**Figure 7.** Moll and Nieder (2015) prospective coding study. a) Crows were trained on a conditional auditory-visual (A-V) DMS task with either a burst of noise or bird song as the sample stimulus mapped on to a blue-square and a red-square, respectively. Following the delay period the crows saw either a red or blue square. A correct match required a response to a matching stimulus. A correct nonmatch required withholding a response until the next, matching stimulus appeared. b) Neural responses from cells in the NCL, an area equivalent to the PFC of primates. Notice this cell fires in the delay period after noise serves as the sample stimulus (dark blue line). Additionally, the cell fires in the delay period on incorrect trials when bird song served as the sample stimulus (light red line). Given that bird song should have elicited a memory of red, and given that the crow performed incorrectly, the fact that the dark blue and light red lines map on to each other is evidence of prospective processing. The neural data are reprinted, with permission, from Moll and Nieder (2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

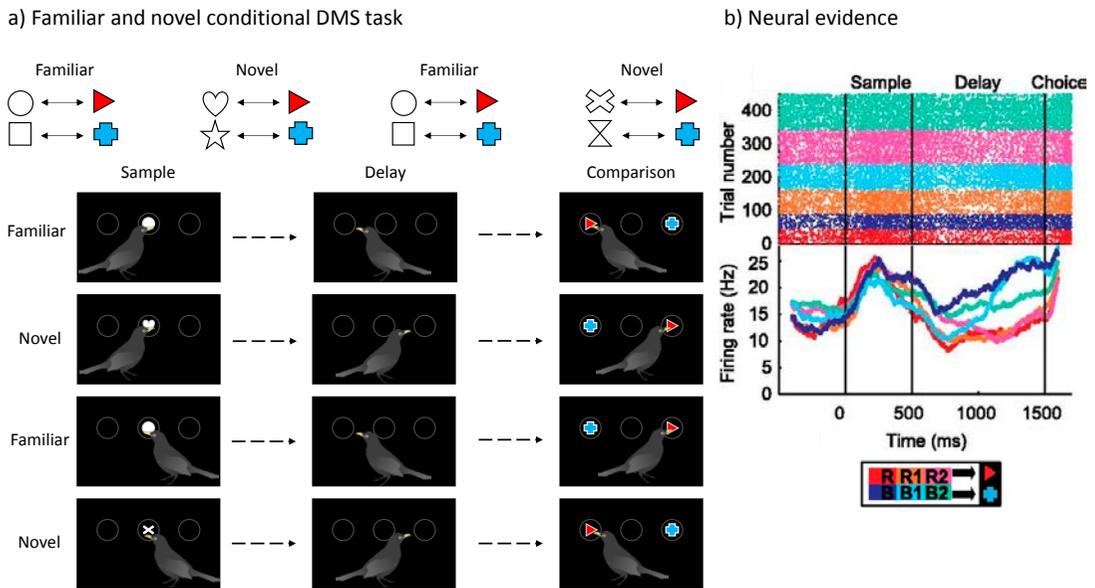
stimulus was a bird song. The animals were actually presented with both red and blue comparison stimuli one after the other (and balanced for order). If the comparison was a match, the crows had to respond to the matching stimulus, whereas if it was a nonmatch they had to withhold a response to the nonmatching stimulus until the correct comparison stimulus appeared. The authors report neuronal activity that correlated with audio-visual associations. Take for example the activity displayed in Figure 7b. This cell showed a slight increase in activity to the noise sample stimulus (solid blue line), and that activity continued to increase throughout the delay period. Similarly, the cell displayed little activity to the sample stimulus when the bird song was played (solid red line), and there was no delay activity following that sample stimulus.

In and of itself, the delay activity following the burst of noise could simply reflect a retrospective code of having heard that sample stimulus. However, two outcomes observed by the authors make a retrospective account less likely. The first outcome was the neural activity on incorrect trials. On incorrect trials, when noise was the sample stimulus (Figure 7b, light blue line) there was little activity during the delay period, but when bird song was the sample stimulus (light red line) there was an increase in activity throughout the delay. Thus the neural activity was more likely a reflection of a prospective code of what stimulus the crow intended to respond to, rather than what stimulus it had just heard. In other words, when bird song was played and the crow got that trial wrong, it was likely thinking of blue, and hence the neural activity to an incorrect bird song trial maps on to the neural activity of a correct noise trial. The second outcome was that when the crows were trained on an auditory DMS task, where they had to match the comparison stimulus to the identical sample stimulus, there was almost no selective delay activity. Thus it was unlikely that the delay activity in the auditory-visual conditional DMS task

represented a retrospective code of the to-be-remembered sample sound, but rather a prospective code of the to-be-responded-to visual comparison stimulus.

More evidence for a neural code of prospective processing came from a study by Veit, Pidpruzhnykova, and Nieder (2015) who trained crows on two conditional DMS tasks. Within a session crows received blocks of either a “familiar” conditional DMS task, one which was the same from session to session, or blocks of a “novel” conditional DMS task, one which differed between sessions as well as between blocks within a session (Figure 8a). In both the familiar and novel blocks, the same comparison stimuli were used, a red triangle and a blue plus. In the familiar conditional DMS task, the same two sample stimuli were used, say circle and square, and they were mapped onto the red triangle and the blue plus. The familiar task was well learned by the birds. In the novel conditional DMS task, a different set of visual sample stimuli mapped on to the red triangle and blue plus, and that set changed from one novel block to the next, and across sessions (e.g., heart and star, then cross and hourglass, etc.). Although the crows were well versed on the familiar task, the novel task required that they learn the correct pairings by trial and error. Remarkably, the birds were able to learn the novel associations within a block of trials, starting around chance and improving to 70-75% correct within about 70 trials.

Veit et al. (2015) found that many neurons showed similar activity pattern in the sample and delay period for sample stimuli associated with the same test stimulus. In other words, the cells responded in the sample and delay periods to the sample stimuli that mapped onto the same comparison stimulus (Figure 8b), an outcome easiest accounted for by arguing that the crows were adopting a prospective code and learning which novel sample stimulus predicted red triangle, and which novel sample stimulus predicted blue plus. This categorical grouping of several sample stimuli based on their learned



**Figure 8.** Veit et al. (2015) familiar and novel conditional DMS experiment. a) The crows were trained on a familiar conditional DMS task with sample and comparison stimuli that never changed. Interspersed within a session of blocks with the familiar stimuli were blocks with novel sample stimuli mapped onto the familiar comparison stimuli. Within a session the crow had to learn the correct pairings of the novel sample stimuli onto the familiar comparison stimuli. b) Neuronal responses from a cell in NCL. In the case of this cell, the crow was trained with a familiar block (see insert, samples R and B), then two novel blocks (samples R1 and B1, and R2 and B2). The cell shown in this example shows delay-period activity following all the samples that are mapped onto the blue plus. Given that the physical appearance of the sample stimuli are all different, but they all map on to the same comparison stimulus, is evidence for prospective processing. The neural data are reprinted, with permission, from Veit et al. (2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

associated test stimulus seemed to mainly occur during the late delay period, and so one might imagine that the crows switched from a sensory-related retrospective coding during the sample and early delay period towards prospective coding of the anticipated target stimulus in the late delay period. Thus, delay activity of crow NCL neurons constitutes a prospective representation of upcoming behavioural choices for both familiar and novel associations (Veit et al., 2015).

### 3.2 Prospective processing of reward information

One of the main roles of the frontal lobe is to monitor and adjust behaviour. One of the first such demonstrations was made by Quintana and Fuster (1992), who trained

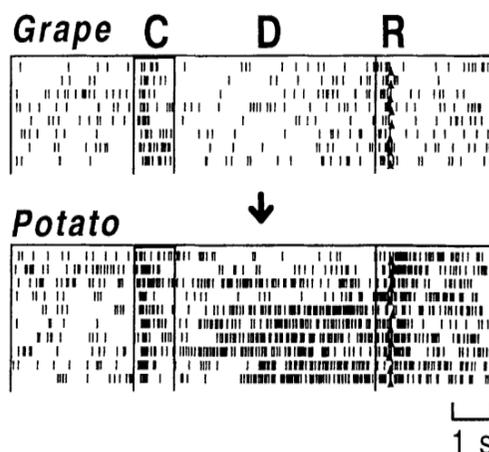
monkeys on a conditional DMS task in which colour sample stimuli were followed after the delay by either the presentation of two white discs, one on the left and one on the right, or two colour stimuli. When yellow and blue served as the sample stimuli, the monkey was 100% certain that the upcoming comparison stimuli would be the two white discs, and that the correct choice was to respond to a particular position (a yellow sample meant respond to the right white disc, whereas a blue sample stimulus meant respond to the left white disc). On the other hand, when red and green served as the sample stimuli, either two white discs could appear, in which case the correct choice was to a position (a green sample meant respond to the right white disc, whereas a red sample stimulus meant respond to the left white

disc), or red and green could appear, in which case the correct choice was to respond to the colour that had appeared as the sample stimulus. Quintana and Fuster (1992) found that some cells exhibited direction-specificity, that is, fired more when the upcoming response was, say, to the right side than the left side. More interestingly, the amplitude of firing was a function of the probability with which the sample stimulus predicted that a direction response would be required after the delay period. Take, for example, a cell that fired selectively to a prospective “right” response, activity that would occur after both the yellow and green sample stimulus. Such a cell would also fire more strongly after a yellow sample stimulus than after a green sample stimulus. In general, the more reliable a certain cue was at predicting a subsequent reward the higher the amplitude of the prospective delay activity.

Watanabe (1996) found similar reward-specific anticipatory neuronal activity in PFC neurons by training monkeys in a spatial delayed-response task with various kinds of food and liquid as reward. Monkeys were presented with a sample stimulus that consisted of either the reward itself (a food item presented behind a transparent screen) or a stimulus that predicted a certain food. Following a delay period, a ‘go’ stimulus indicated that the monkeys had to respond to the side in which the sample had appeared to obtain the reward. Watanabe (1996) found that certain cells in PFC fired differentially in the delay after the animal had seen certain food items. Such activity could reflect a prospective code of the anticipated reward, but it also could reflect merely the continuation of activity in the delay period to the activity to the sample stimulus. In other words, if a cell fires differentially to the presentation of an apple as the sample compared to raisin as a sample, the delay activity to apple (and not to raisin) may simply reflect a continuation of the activity to the sample stimulus, that is, a retrospective code. However, a retrospec-

tive account is less likely in situations observed by Watanabe (1996) when a cue predicts a certain reward, such as a red stimulus predicting the presentation of an apple, especially when the cell did not respond to the red stimulus when it served as a cue.

But perhaps the best evidence in favor of a prospective code occurred when Watanabe (1996) delivered an unexpected reward. In one situation, Watanabe (1996) changed the predicted reward from a grape to a potato (Figure 9). Initially, this cell did not fire in the delay period (D) after the cue (C) that predicted a grape reward, though it did fire transiently once the grape was presented as a reward. When the cue now predicted a potato reward, there was still no neural activity in the delay period on the first trial, nor would one expect there to be since the delay period occurs before the animal first received the



**Figure 9.** Reward study by Watanabe (1996). The cell did not fire in the delay period to the cue that predicted an upcoming grape reward (top panel). The reward was then changed to potato. In the first trial the cue would still have predicted a grape reward (because the animal had not yet experienced the change in reward). By the third trial, the animal had learned that the cue now predicted a potato reward. Given that the cue remained the same and that the nature of the upcoming reward had changed, the delay activity reflects a prospective code of the animal thinking about the upcoming potato reward. The neural data are reprinted, with permission, from Watanabe (1996).

unexpected potato reward. There was, however, a strong response to potato in the reward period, thus we could assume that this particular cell fires to an image of a potato. The cell continued not to fire in the delay period on the second trial, but from the third trial onwards the cell displayed a vigorous response in the delay period after the cue that now predicted potato, and a vigorous response to the potato when it was delivered as a reward. The activity of this cell is strong evidence that the animal was prospectively anticipating a specific rewarded event.

#### 4. Prospective processing in primates and birds

The findings presented in sections 3.1 and 3.2 are firm neural evidence of prospective processing in primates and birds, at least with respect to the monitoring of future behaviours. A hallmark of cognition lies not only in the ability to monitor one's current or future behavior, but also in its ability to adjust one's behaviour to suit changing circumstances. The ability to adjust one's behavior is central to the notion that the frontal lobes are important for executive control. Neural evidence for such adjustment has been observed in humans. For example, Braver, Paxton, Locke, and Barch (2009) noted that under specific training circumstances, the neural profile of PFC activity in older adults adjusted towards that of younger adults. Indeed, the authors argue that the neural activity of the young adults and that of the trained older adults reflected expectancies across trials, a form of prospective processing.

Neural evidence for adjustment has not been examined as closely in nonhumans. That said, we have reported neural evidence of executive control in pigeons trained on a directed-forgetting DMS task in which one cue instructed the animals to remember the just-seen information, whereas another cue instructed the animals to forget the just-seen information (Rose & Colombo, 2005). The neural activity in the delay period adjusted to whether the animal needed to remember information: when told to remember the

delay activity remained sustained throughout the retention interval, whereas when told to forget the delay activity reverted to baseline levels. Thus, whatever the neural mechanism underlying adjustment of behavior, there seems little reason at present to doubt that it exists in both primates and birds.

On a broader level, the neural evidence presented in sections 3.1 and 3.2 may give the impression that crows and monkeys stand apart from rats and pigeons in their ability to engage in prospective processing. In fact, there is little evidence to support the claim that there are qualitative differences between monkeys, crows, rats, and pigeons with respect to behavioural underpinnings of prospective processing (see Cook, Brown, & Riley, 1985, for a wonderful example of prospective processing in rats). The lack of neural evidence from pigeons is more due to a lack of studies than a lack of ability. Indeed the commonality across primate and avian species is perfectly in line with Macphail's (1985) view, and indeed recent views, that there are little differences between monkeys and pigeons in terms of abstract numerical reasoning (Scarf, Hayne, & Colombo, 2011), conceptual behavior (Colombo, Cottle, & Frost, 2003), and serial-order behavior (Scarf & Colombo, 2010). The similarity between monkey and birds in prospective processing, therefore, may represent a case of convergent evolution. Whether certain selective pressures drove the emergence of prospective processing, or whether prospective processing is an emergent quality of a memory system that has achieved a certain "critical mass" of neurons (cf. Güntürkün, Ströckens, Scarf, & Colombo, 2017), remains to be determined.

#### 5. Summary

We present both behavioural and neural evidence in support of the view that animals can engage in prospective processing. *What drives an animal to engage in either retrospective or prospective processing?* Surely whether an animal chooses to engage in retrospective or prospective processing is not

an all-or-none phenomenon, and is influenced by a number of factors such as memory load (Cook, Brown, & Riley, 1985), stimulus discriminability (Urciuoli & Zentall, 1986), as well as sample-comparison contingencies (Honig & Thompson, 1982) and stimulus modality (Colombo & Graziano, 1994). In some situations, within the same session or trial, an animal may shift from using one strategy to another in an effort to minimize the load on memory (Cook, Brown, and Riley, 1985). One thing is clear, and that is that there is ample evidence that animals engage in prospective processing, both behavioural and neural. The fact that animals can look ahead and anticipate an event places them in a league close to humans with respect to this ability. Whether they can engage in true mental time travel and recreate a past event unprompted, or whether they can engage in the ultimate form of mental time travel, episodic memory, remains to be seen, although the evidence is very suggestive (Clayton and Dickinson, 1998).

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