

**Working Memory in Crows (*Corvus Corone*):
Attention and Cognitive control**

Inaugural Dissertation
zur
Erlangung des Grades eines Doktors der Naturwissenschaften
in der
Fakultät für Psychologie
der
RUHR - UNIVERSITÄT BOCHUM

vorgelegt von
Erica Fongaro

aus Bochum

Bochum, April 2019

Referent: **Dr. Jonas Rose**

Korreferent: **Prof. Dr. Onur Güntürkün**

Tag der mündlichen Prüfung: 01.08.2019

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Voraussichtlicher Termin der mündlichen Prüfung:

Declaration

I certify herewith that the dissertation included here was completed and written independently by me and without outside assistance. This work has never been submitted in this, or a similar form, at this or any other domestic or foreign institution of higher learning as a dissertation. The abovementioned statement was made as a solemn declaration.

Name / Signature

ERICA FONGARO

Bochum, 12th of April 2019.

The function of memory is not only to preserve, but also to throw away. If you remembered everything from your entire life, you would be sick.

Umberto Eco.

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List of Abbreviations

AP	anterior-posterior
DMTL	delayed-matching to location task
FEF	frontal eye field
fMRI	functional magnetic resonance imaging
IHC	immunohistochemistry
IPS	intraparietal sulcus
ITI	inter-trial interval
IES	inverse efficiency score
vINCL	ventrolateral nidopallium caudolaterale
LIP	lateral intraparietal area
LTM	long-term memory
mNCL	medial nidopallium caudolaterale
NCL	midopallium caudolaterale
NCM	caudal medial nidopallium
PEV	percentage explained variance
PFC	prefrontal cortex
PPC	posterior parietal cortex
STM	short-term memory
TH	tyrosine
WM	working memory

Abstract

Working memory (WM) is a key component in the update, maintenance and manipulation of information through attention and executive control. The presence of those mechanisms can grant an efficient coordination of memory resources measured as WM capacity. A recent study demonstrated that this capacity is comparable between crows and monkeys (Balakhonov & Rose, 2017). In my thesis, I investigated in crows the presence of control mechanisms of WM as attention and executive control. In the first chapter, we explored attention and executive control over WM in crows. We trained two crows (*Corvus corone*) in touchscreen-equipped operant chambers on a change detection task. We used pre- and retro-cues to direct attention to a spatial location in a 2, 4 or 6 sample-array, in combination with no-cue conditions. We found a significant benefit of cueing for both pre- and retro-cues compared with no-cue conditions, according to the behavioral costs in the different memory load conditions. These results showed that crows, like humans could utilize attentional cues (pre-cue) to efficiently direct attention to critical stimuli. Importantly, the crows could also utilize cues to improve WM capacity, even after the stimuli were already held in WM and no longer present on screen (retro-cue): this demonstrated a previously unseen form of control mechanism over information in crows. By restraining their attention and managing the accessibility of the relevant information, crows mitigated their WM capacity.

Using the most challenging WM load (3-items in one hemifield), our crows played the same task in the second chapter while recording single-cell activity from the vLNCL, an functionally involved in WM task (Ditz & Nieder, 2015, 2016; Moll & Nieder, 2015; Veit, Hartmann, & Nieder, 2014; Veit, Pidpruzhnykova, & Nieder, 2015; Veit & Nieder, 2013). Simultaneously, we also recorded for the first time in the recent discovered mNCL, to elucidate its implication in WM (von Eugen, 2017; Sen et al., 2019). The task included pre- and no-cue conditions and the crows confirmed the cue effect. In vLNCL, we found neural correlates of attention that mirrored the behavioral benefits: on cued-stimuli, attention enhanced the neuronal information for color and location compared to uncued and to irrelevant stimuli. This enhancement was during all the WM processes of the color information, from the encoding to the retrieval. Importantly, the vLNCL controlled attention to improve location information within WM, in the absence of stimuli, and facilitated an increased color information in the encoding of the comparison color at the cued location. Oppositely, the

mNCL was not engaged in WM processes under the tested visual domain. Our data demonstrated the neural mechanisms by which information held in WM were enhanced under attentional mechanisms in the corvid vLNCL, confirming the role of the area in higher order cognitive functions.

In the third chapter, we investigated the executive control abilities in crows during a WM task. Two crows performed a delayed-matching to location task to optimize the reward magnitudes. In order to perform the task, the crows had to hold simultaneously multiple items, with color and locations features. They had to retrieve reward magnitudes to memorize spatial information and to make a decision over those contents in WM. The crows' performance revealed ability and limits in controlling the online information in WM, showing their efficiency in executive control mechanism when triggered by more beneficial reward magnitudes. Following a distance effect, the rewards discriminability was more effective increasing the difference between reward magnitudes.

This thesis show that the cognitive capacity of corvids is limited like in humans by both attention and executive control of the WM system. The behavioral and the neural similarities open up at a general constraint of neural processing in which WM, through attention and executive control, monitors its resources improving the performance.

GENERAL INTRODUCTION

Memory is one of the most complex and fascinating mystery of human mind. It is a fundamental part of our life which builds and preserves, our individuality every day. Memories drive our decisions and our actions. It teaches us to learn from the past to plan the future.

Memory has allowed entire populations to transmit their own identity through the centuries, even before the invention of writing. For Aeschylus, memory is the "mother of all wisdom" (Carr, 2001), for Quintilian it is "the art that preserve all the other arts" (Fantini, 2011). For Plato is knowledge (Sassi, 2007) and Cicero describes it as "the guide to life" (Fantini, 2011).

In the common sense, as in literature, the "voluntary" memory recalls an intentional reminiscence of past episodes. The "involuntary" memory, described by Proust in the novel "In search of lost time", is any stimulus (the sight of an object, a perfume) which could irrationally return the past and make it live again in the present (Proust, 1989).

This extraordinary faculty continues to attract the curiosity of poets, philosophers and scientists from antiquity to today. Although, cognitive psychology and neuroscience have not yet fully understood all the mechanisms that form and govern memory, many important goals have been achieved.

Types of Memory

In the 1960s, Atkinson and Shiffrin (1968) (Fig. 1A) postulated the existence of three types of memory: sensory memory, short-term (STM) and long-term (LTM) memory (Atkinson & Shiffrin, 1968). Memory is divided based on the duration of the preserved memory. Sensory memory stores information from the senses and holds them for few milliseconds. A common example of sensory memory occurs when you visualize an object with closed eyes, right after you stared at it. That image you "see" in your mind is your iconic memory of that visual stimuli, which lasts for milliseconds and quickly fades. This is because "iconic memory" is part of the visual sensory store. Sensory memory is not involved in higher cognitive functions like short- and LTM, because it is not consciously control (Atkinson & Shiffrin, 1968).

STM, instead lasts for few seconds and can hold only few information. After this time, the trace decays, unless this information is transferred to the LTM (Atkinson & Shiffrin, 1968). Thereby, STM represents a transient between sensory memory and LTM. The memory trace can be consolidated through behavioral strategies, like rehearsal (Janse, 2018). An example of rehearsal would be repeating a number until you could write it down. If you are interrupted during your rehearsal, you can easily forget the number, since it is only in your STM. LTM can store an indefinite amount of information for an unlimited time (Cowan, 2008). There are many types of LTM. It is subdivided into explicit and implicit memory. Explicit memory requires conscious recall of episodic memory (memories of events) and semantic memory (general knowledge) (Ullman, 2004). In contrast, implicit memory stores memories not based on consciously retrieving information but on implicit learning of motor, perceptive and cognitive abilities (i.e. learning motor skills, like learning to ride a bike) (Schacter, 1987).

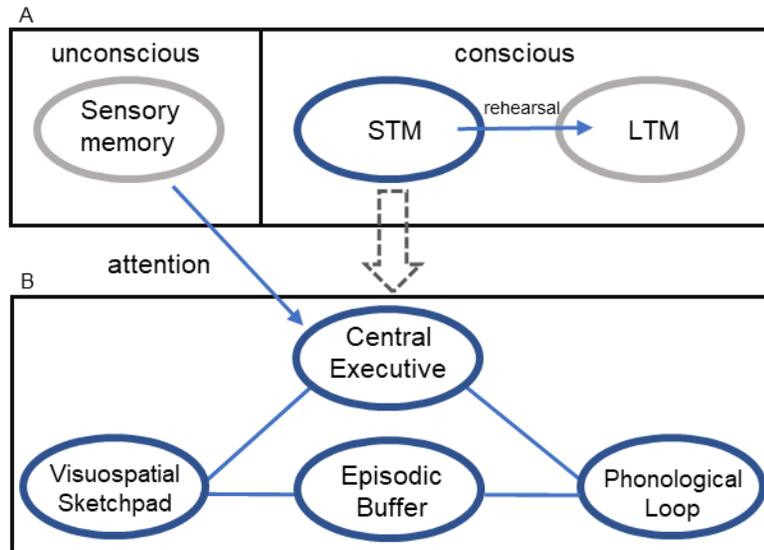


Figure 1. Memory models.

A) Atkinson and Shiffrin (1968) model of memory: the model is made of three different memory stores: the sensory memory, the short-term memory (STM) and the long-term memory (LTM). The STM is a limited capacity store to place the sensory memories to be rehearsed. Only rehearsed items in STM can enter LTM. B) Baddeley (2000) working memory model: the STM is now composed by three main components: the central executive which acts as supervisory system and controls the flow of information to its subsystems: the phonological loop, the visuo-spatial sketchpad and the episodic buffer. Attention is at the source of the WM process.

1. Working Memory

In the following years, the model of Atkinson and Shiffrin started downsizing itself because of several criticisms concerning the STM (Baddeley, 2011; Craik & Lockhart, 1972). This model proposed that information from the environment passed through a series of brief sensory memories in the perception process before reaching a STM (Peterson & Peterson, 1959). An arguably simplify view that operate in a single, uniform fashion to explain the learning processes (Baddeley, 1996; Craik & Lockhart, 1972): holding information in STM would guarantee transfer to LTM. Consequently, the STM limited capacity was the bottleneck for registering new information in LTM (Baddeley, 1996).

In the light of further scientific developments, Baddeley and Hitch introduced the working memory (WM) model in 1974 (Baddeley & Hitch, 1974) as an alternative and more specific model to Atkinson and Shiffrin's STM (Baddeley, 2000). WM is still a STM that maintains information in a limited time, but in addition the model highlights its ability to process that information (Baddeley & Hitch, 1974). Thus, the WM maintains and processes the information during the execution of cognitive tasks (Cowan, 2014). It keeps the information actively at the service of other cognitive processes involved in carrying out a task. In order to fulfill this function, it is indispensable the "central executive", which controls the flow of information. The central executive is responsible for both the attentive resources and manipulation of information (Baddeley & Hitch, 1974). Furthermore, it controls over two auxiliary subsystems: the "phonological circuit" which maintains verbal information and the "visuospatial sketchpad", which processes and stores visual and spatial information (Baddeley, 1986).

In 2000 Baddeley, after observing some patients with LTM deficits but good short-term recall (Daneman & Carpenter, 1980; Daneman & Merikle, 1996; Engle, Tuholski, Laughlin, & Conway, 1999), added a fourth component to the model of WM (Fig. 1B): the "episodic buffer" (Baddeley, 2000). The episodic buffer is configured as a limited capacity system directly connected with the information coming from the other subsystems and from the LTM. It can hold multidimensional information, serving as an important mediator between perception, WM and LTM (Baddeley, 2000).

1.1. Working Memory Capacity

An important peculiarity of WM is that it is limited (Cowan, 2010). Only a limited number of items can be hold at the same time and it varies from person to person (Cowan, 2010). It is challenging to determine the real capacity limits because multiple mechanisms are involved in retaining different information (Baddeley & Hitch, 1974). According to George Miller a person can retain process only seven (7 ± 2) items of information (which could be letters, digits, or words) in a correct serial-order in WM (Miller, 1956). The number seven became a public truth, even if Miller himself defined it as "a pernicious Pythagorean coincidence" (Miller, 1956).

Allan Baddeley and colleagues showed that this number could vary not only by the number of words to remember, but also by their lengths (Baddeley & Hitch, 1974). In the meantime, Donald Broadbent took a different approach to reveal the “magic number” and questioned how many elements can be remembered naturally, without any strategy (Broadbent, 1958). When holding three elements, memory is almost error free. Adding other elements, the information in WM is impaired. Hence, Broadbent proposed to replace the magical number seven with the magic number three (Broadbent, 1958). Subsequently in 2001, an updated research by Nelson Cowan suggested the number four, to be the limit in WM. This “semi-magic number” is universal for all healthy individuals and any type of modality with the size of the information varying (Cowan, 2001).

1.2. Working Memory, Attention and Executive Control

The limited capacity of four chunks (Fig. 2A) assigned great importance to mechanisms of attention and activation (Cowan, 2001). The limited capacity of WM lies in the focus of attention, which can keep up to four information (Cowan, 2005). According to this model, WM consists of activated representations that fall within the focus of executive control, which can host up to four elements at a time. In this way, the role of the attentional focus and the activation levels is emphasized (Cowan, 2005). At the source of WM, the information stays within the focus of attention, which enhances processing of one information at the expense of another. The activated memory keeps the information in order to complete a task. The central executive or the “executive control” gathers those mental processes together in an online-way that can be modified by instructions and incentives. The executive control manages the focus of attention, setting attentional limits to WM based on time and capacity constraints. It does not control subsidiary system, like in previous models (Baddeley & Hitch, 1974). In summary, WM uses attention to ensure the selection of basic elements and the central executive as director.

The number of information in the focus of attention depends on what is needed in the specific moment, hence on what the executive control maintains for the current behavior. The model indicates the necessity to allocate WM resources more efficiently and profitably due to its limited capacity and due to the fact that the relevance of the information may change. Thus, WM allocates and re-allocates resources, and processes the most relevant representations for the current behavior through

attention and executive control (Brady & Hampton, 2018; Chun, Golomb, & Turk-Browne, 2011; Cowan, 2010; Myers, Stokes, & Nobre, 2017; Unsworth & Engle, 2007).

1.2.1. Working Memory and Attention

Attention refers to the process of selection of some information at the expense of others (Pashler, 1998). Primarily involved in the selection of the information, attention reduces the input to a manageable amount (Marchetti, 2014), acting at different memory stages of the information in WM (Gazzaley & Nobre, 2012). Information goes through encoding, storage, and retrieval (Klein, 2015). Encoding is the first memory stage that receives and processes information. This stage transfers information from the outside world to interact with our senses by means of chemical and physical stimuli. The encoded information are stored through the maintenance stage and finally, the retrieval (or recall) accesses the information from the maintenance stage (Jonides et al., 2008). Problems can occur at any stage of the process, like the presence of distractors, weak maintenance or the incapacity to retrieve information once stored. Specifically, when insufficient attention is paid during the encoding or the retrieval of an information, forgetting is likely to happen (Levin & Simons, 1997). To prevent this, humans use attention to increase processing efficiency (Posner & Cohen, 1984). Selective attention exerts its control by prioritizing the encoding of information toward the items that are the most relevant to the current processing goals (Ku, 2018). By filtering out contextual distracters, attention is a “gatekeeper” (Broadbent, 1958) for WM (Awh, Vogel, & Oh, 2006; Carrasco, 2011; Yantis, 2008) to properly select information that will be processed. Activity in the visual system can be modulated by attention (Boynton, 2005; Carrasco, 2011; Treue, 2001), which allows the organism to adequately cope with contextually and behaviorally relevant information. In this way, attention can affect early perceptual processing (Cherry, 1953; Mangun & Hillyard, 1991). The pioneer work from Posner and Cohen (1984) proved that using attention through a visual cue at the location of a target facilitates its detection, compared to the locations without visual cues (“no-cue”) (Posner & Cohen, 1984). A prominent example is a spatial “pre-cue”, where a centrally presented arrow indicates the likely location of the subsequent target (Chun, 2000; Pertzov, Bays, Joseph, & Husain, 2013; Posner, 1980). The so-called, “cue effect” enhances performance, accuracy and detection rate in WM tasks (Carrasco, 2011; Castiello & Umiltà, 1990; Posner, 1980).

Interestingly, recent findings have shown that attention acts not only at the perceptual representation but also at the later stages of WM, like during maintenance or retrieval of the information (Fougnie, 2008; Osman & Moore, 1993; Souza & Oberauer, 2016). Cueing items after stimulus onset (“retro-cue”), after the stimuli have disappeared, has a similar empirical advantage (Astle, Nobre, & Scerif, 2012; Berryhill, Richmond, Shay, & Olson, 2012; Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; Makovski, 2012; Makovski & Jiang, 2007; Sligte, Scholte, & Lamme, 2008, 2009). Since this effect cannot be driven by sensory gate-keeping of attention, it must rely on some form of control mechanism over WM, enable to shift attention among WM representations.

1.2.2. Working Memory and Executive control

Mechanisms of control of WM rely under the name of executive control. The executive control is responsible for controlled processing in WM, including (but not limited to) directing attention and maintaining task goals (McCabe, Roediger, McDaniel, Balota, & Hambrick, 2010). It operates attention, the memory trace and the environment in an integrative manner to guide choice among several options in order to achieve a goal (Anderson, 2002).

The executive control enables the WM system to attend some stimuli and ignore others. Its role is to ensure the maintenance of attention on the necessary information and the inhibition of those irrelevant ones (Buchweitz 2008). The executive control can shift, update and inhibit information in WM (Dempster & Corkill, 1999; N. Morris & Jones, 1990; Shilling, Chetwynd, & Rabbitt, 2002; Smith & Jonides, 1997). It acts more like a system that controls attentional processes rather than as a memory store, like the phonological loop and the visuospatial sketchpad. The shifting attention within WM information, involved in the retro-cue effect mentioned before, is a type of executive control (Berryhill et al., 2012; Brady & Hampton, 2018). The executive control comes into play for example during dual-tasks, tasks that simultaneously engage the phonological circuit and the visuospatial notebook or in tasks that simultaneously require storage and processing of information (Dehn, 2015; Tronsky, 2005). Hence, the executive control in WM integrates information from the phonological loop and the visuospatial sketchpad, and draws on information held in LTM. Overall, the executive control supervises the memory stages in WM, to prevent any failure in the information

processing (Fougnie, 2008; McCabe et al., 2010). The importance of executive control gives a volitional nature to WM. The updated version of the WM model of Miller, splits the "memory" part as a mechanism for online maintenance of information, and the "working" part as volitional control over it, selecting what to stream into the information process (Miller, Lundqvist, & Bastos, 2018).

2. The Prefrontal Cortex

In mammals, WM is primarily executed by the prefrontal cortex (PFC), an area identified as the seat for controlling executive functions (Cohen, Braver, & Brown, 2002; Fuster, 2000; Goldman-Rakic, 1996; Güntürkün, 2005; Miller & D'Esposito, 2005; Miller, 2000). The PFC is one of the prime targets of dopaminergic innervation in the mammalian brain (Miller, 2000; Fuster, 2008). It receives rich dopaminergic innervations from the ventral tegmental area and substantia nigra and noradrenergic and serotonergic innervations from the locus ceruleus and dorsal raphe nuclei respectively (Gaspar, Stepniewska, & Kaas, 1992; Arnsten and Robbins, 2002). The PFC is situated in the anterior part of the cerebral cortex and is an associative zone characterized by multimodal convergence (Petrides and Pandya, 2002; Pandya & Yeterian, 1990). It receives afferents from all sensory association areas, from hippocampus, amygdala, hypothalamus, pons and tegmentum (Petrides and Pandya, 2001; Fuster, 2008) and from several thalamic nuclei (most notably the projection from the mediodorsal nucleus) (Barbas, 2009; Preuss, 1995). The PFC sends efferents to the striatum and all secondary motoric structures, like frontal eye field (FEF) and premotor cortex (Fuster, 2008). This developed connectivity pattern places the PFC in the ideal position to broadly influence cognitive processing and to exert "top-down-control" (Fuster, 2000; Miller & D'Esposito, 2005).

As prominent functions of the PFC, WM has often been used for functional segregation. Several researchers attributed to the dorsal PFC the maintenance of spatial information and to the ventral PFC the maintenance of non-spatial information (Goldman-Rakic, 1996; Levy & Goldman-Rakic, 2000).

At neuronal level, early electrophysiological studies in the PFC attempted to define the neuromodulation of WM (Fuster & Alexander, 1971; Kubota & Niki, 1971). Neurons in the PFC of monkeys showed increased firing during the delay period of WM-tasks (Fuster & Alexander, 1971; Kubota & Niki, 1971). Therefore, those cells, described for the first time by Kubota and Fuster,

were later called “delay cells” and interpreted as a neural correlate of WM. The idea was that a WM-task information needs to be maintained to span a delay as an active delay activity spiking to maintain the information in WM (Miller et al., 2018). Since this discovery, a lot of research was dedicated to delay cells and they were described in several cortical and subcortical structures (Erlich, Bialek, & Brody, 2011; N. Li, Daie, Svoboda, & Druckmann, 2016; Liu et al., 2014; L. Wang et al., 2015). In spatial WM tasks, Funahashi et al. (1989) showed that delay cells can be spatially tuned and fire preferentially for a preferred cue direction (Funahashi, Bruce, & Goldman-Rakic, 1989). The response of these cells was maximal when the animal needs to memorize one spatial location and deteriorated when increasing the distance of the memorized location from the ideal location. This persistent firing in the delay activity is proposed to be the neurological substrate of WM (Funahashi et al., 1989; Goldman-Rakic, 1996).

One important difference between delay cells in PFC and in other parts of the brain was reported by Miller et al. (Miller, Erickson, & Desimone, 1996). The authors showed a peculiarity of delay cells in PFC: their action against interference. Two monkeys performed a serial delayed-matching to sample task with interfering stimuli during the delay period. They found that prefrontal delay activity is resistant against interference while temporal delay activity is not.

Moreover, information about the reward association directly modulates the activation of delay cells in PFC (Watanabe, 1996). After integrating all the different sensory information of a stimulus, the prefrontal delay activity interests the maintenance of sensory information (Lebedev, Messinger, Kralik, & Wise, 2004; Gregor Rainer, Rao, & Miller, 1999).

Further studies in primates revealed that WM tasks activated, additionally to the PFC, also the hippocampus and posterior parietal cortex (PPC). Those areas cooperate in a network organization with other cortical and subcortical structures as an integrated unit (Friedman & Goldman-Rakic, 1994; Miller et al., 2018).

In WM tasks, selective attention is of considerable importance not only for gating the encoding of task-relevant items into WM (Gazzaley & Nobre, 2012; Murray, Nobre, & Stokes, 2011; Rutman, Clapp, Chadick, & Gazzaley, 2010; Schmidt, Vogel, Woodman, & Luck, 2002; Zanto & Gazzaley, 2009) but also in shaping WM maintenance, accordingly to changing task goals (Kuo, Stokes, & Nobre, 2012). This attentional effect has been seen by Lebedev et al. (2004). He found that the prefrontal delay cells were involved in attentional selection. These data are consistent with the idea

proposed by Awh and Jonides (2001). In this model, the PFC uses selective attention to act in a “top-down” modulation and guide the maintenance of sensory information in specialized areas of the brain for that type of information. Evidence from single-unit recordings in monkeys demonstrated sustained firing for neurons that are selective for the specific memoranda throughout the maintenance period in a delayed-match-to-sample task (Chelazzi, Duncan, Miller, & Desimone, 1998; Li, Miller, & Desimone, 1993; Supèr, Spekreijse, & Lamme, 2001). Different subregions of the PFC serve as a source of attention-related signals: the lateral PFC, the frontal eye field (FEF) and the supplementary eye field (Posner & Petersen, 1990; Yantis, 2008). Those areas serve to control stimulus-related perceptual codes in the specific sensory areas and modulate the maintenance of information in WM (Awh & Jonides, 2001; Chelazzi, Miller, Duncan, & Desimone, 1993; Druzgal & D’Esposito, 2001; Harrison & Tong, 2009; Li et al., 1993; Munneke, Heslenfeld, & Theeuwes, 2010; Pasternak & Greenlee, 2005; Serences, Ester, Vogel, & Awh, 2009; M. Stokes, Thompson, Cusack, & Duncan, 2009).

The relationship between WM and executive control recalls a long-range communications between PFC and other cortical areas for the maintaining of specific information (Lara & Wallis, 2015), that make it difficult to study at single-neuronal level. Nowadays, more sophisticated techniques of analysis and measurement of neural activity can study the WM network from multiple-electrodes recordings as local field potential (LFP), the summed activity of many neurons (Miller et al., 2018). During WM tasks, there are different LFP oscillations involved. The alpha and beta bands (10-30 Hz) has been related to top-down information and with inhibitory functions (Miller et al., 2018). The alpha and theta bands (4-8 Hz) of PFC are correlated to the increase of the spatial precision of a change detection task (Lara & Wallis, 2015). The gamma band (30-100 Hz) has been associated with sensory information (Bastos, Loonis, Kornblith, Lundqvist, & Miller, 2018; Honkanen, Rouhinen, Wang, Palva, & Palva, 2015; Roux, Wibrat, Mohr, Singer, & Uhlhaas, 2012; Sederberg, Kahana, Howard, Donner, & Madsen, 2003) and the number of objects held in WM (Roux et al., 2012; Sederberg et al., 2003). A recent study by Ludqvist et al. (2018) showed a specific pattern of interplay between those wave frequencies. When the information needs to be stored, beta was decreasing to allow an increase in gamma frequencies. On the contrary, when the information

could be discarded, beta increased, and gamma decreased. This pattern did not occur when the animal was doing a mistake (Lundqvist, Herman, Warden, Brincat, & Miller, 2018; Lundqvist et al., 2016).

More work is needed to shed light on the precise nature of the interaction between PFC and the WM system. Given that attention and executive control are dynamic processes for an effective WM system, a promising idea should be to try to investigate both the sensorial and the internal representations. The contribution of attention and executive control in WM representations may involve similar neural codes to those that mediate perceptual information (Astle, Scerif, Kuo, & Nobre, 2009; Gratton, 1998; Jiang, Olson, & Chun, 2000; Kuo, Rao, Lepsien, & Nobre, 2009).

3. The Crows: a new animal model for Working Memory

Many researches (Engle & Kane, 2003, 2004) developed models that confirm the relationship between WM and intelligence specifying two important points: fluid intelligence is predicted by WM tasks and the capacity of WM constitutes a good predictor of fluid intelligence. To date, WM studies are conducted primarily on humans and non-humans primates (Pasternak & Greenlee, 2005). In humans, neuropsychological studies yielded a number of interesting results regarding the deficits of cognitive performance in various psychiatric disorders (Schmauss, 2009). Neuroimaging and electrophysiological studies have powerfully illuminated the anatomic areas and the functional aspects of the neural processes underlying attention and WM (Clayton & Emery, 2015). However, those methods have significant practical limitations, concerning, for example, real-time social interactions or the solution of cognitive problems that cannot be studied inside a scanner. Nowadays, those techniques have much improved, but still penalized by poor spatial and temporal resolution, especially when compared to invasive techniques on animals. The only invasive method in humans is transcranial magnetic stimulation (TMS), although through recording from neurons of clinical patients (Clayton & Emery, 2015). Therefore, to examine the neural mechanisms of these cognitive processes, we are still dependent on using animal models, taking advantages of a control manipulation of different brain areas (Schmauss, 2009). The majority of animal studies on higher cognitive functions relies on research on primates in order to profit from anatomical and cognitive synergies

(Phillips et al., 2014). However, monkeys are expensive and the work is under ethical restriction (Clayton & Emery, 2015). Nevertheless, advances in understanding the neuronal mechanisms of WM often occur when studying simpler mammals, like rodents. Rodent models for WM are being increasingly explored since they have the potential to complement primate studies in many ways (Fassihi, Akrami, Esmaeili, & Diamond, 2014). At molecular levels, genetic variations have been shown to correlate with impaired performances in WM tasks (Bertolino et al., 2006; Blasi et al., 2015; Egan et al., 2001; Fan, Fossella, Sommer, Wu, & Posner, 2003; Glickstein, Hof, & Schmauss, 2002). Moreover, brains of rodents are readily available for high-resolution anatomic studies on cognitive network activation, from the global network to the cellular identifications (Laubach, Amarante, Swanson, & White, 2018). In rats, WM has been limited to match- or nonmatch-to-sample tasks (Grobe & Spector, 2006; Peña, Pitts, & Galizio, 2006) and navigation tasks (Jadhav, Kemere, German, & Frank, 2012; R. Morris, 1984). The disadvantages for rodents, concerning cognition, are the limited WM capacity with a short span of time (Dudchenko, 2004) together with distractibility. Those disadvantages are not present in a new animal model for neuroscience: the crow. If the capacity of the WM constitutes a good predictor of fluid intelligence (Clayton & Emery, 2015; Cowan, 2010; Engle & Kane, 2004; Engle et al., 1999), a recent study by Balakhonov and Rose (2017) includes the striking proof that credits all the latest scientific interests in crows. In the study, crows played a similar task previously used to define the capacity limits in monkeys (Buschman, Siegel, Roy & Miller, 2011). The crows performed a change localization paradigm with different WM-load (2, 3, 4 and 5 items), demonstrating a capacity limit of four items, like in monkeys and similar to healthy human (Cowan, 2001; Drew & Vogel, 2009). With this memory capacity, the recent scientific discoveries on their advanced cognitive abilities are not surprising (Taylor, 2014; Vonk, 2015). If mice rely on olfactory stimuli, crows rely mostly on visual and acoustic stimuli, like humans (Bugnyar & Kotrschal, 2004). Ravens can follow human eye gaze to navigate mazes successfully (Bugnyar Thomas, Stöwe Mareike, & Heinrich Bernd, 2004) and to understand the capabilities and limitations of others (Bugnyar & Kotrschal, 2002; Marzluff, Walls, Cornell, Withey, & Craig, 2010). They have an internal conception of the knowledge of specific others and this might be related to the concept of empathy (Fraser & Bugnyar, 2010; O'Connell, 1995). Magpies recognize themselves in mirrors (Prior, Schwarz, & Güntürkün, 2008). Crows usually choose their partner for a lifetime, but they also participate in larger social assemblies for sharing information, sleeping and for hunting.

Crows are able to count (Ditz & Nieder, 2015), show episodic memory and plan for the future (Clayton, Bussey, & Dickinson, 2003). They are well-known for their creativity (e.g. dropping walnuts on streets, where they are cracked by vehicles running over) and famous for using tools (Bluff, Troscianko, Weir, Kacelnik, & Rutz, 2010), especially the New Caledonian crows (Auersperg, Bayern, Gajdon, Huber, & Kacelnik, 2011; Knaebe, Taylor, Elliffe, & Gray, 2017; Taylor, Hunt, & Gray, 2012). All these behaviors require higher-order processing and are all signs of executive functions (Kirsch, Güntürkün, & Rose, 2008), in which WM represents the core.

Already most behavioral paradigms used in corvids research tap into WM. Some examples are the delayed-matching to sample task or WM tasks (Balakhonov & Rose, 2017; Ditz, Kupferman, & Nieder, 2018; Ditz & Nieder, 2016; Goto & Watanabe, 2009; Moll & Nieder, 2015; Veit et al., 2014), widely used for testing visual WM and WM capacity in animals. The Aesop's Fable paradigm (Logan, Jelbert, Breen, Gray, & Taylor, 2014) investigates causal understanding, the process of identifying the relationship between a cause and its effect. The food-caching paradigm (Clayton, Dally, & Emery, 2007) studies spatial WM and the string-pulling paradigm (Heinrich & Bugnyar, 2005; Taylor et al., 2010) tests spontaneous problem solving (Jacobs & Osvath, 2015).

Although, crows have been proven their abilities in many WM paradigms, the components that rule an efficient performance remains unexplored. Attention and executive control are the components that grant the control of WM resources. Given the corvid WM capacity (Balakhonov & Rose, 2017), the existence of similar mechanisms can be studied across behavioral and electrophysiological measurements at different WM stages and challenging loads.

3.1. The avian prefrontal cortex: the Nidopallium Caudolaterale

Crows are by no means close relatives of humans: our most recent common ancestor lived in the Permian 320 million years ago and despite this great distance, they show remarkable cognitive abilities (Emery & Clayton, 2004; Kirsch et al., 2008). Their intelligence must have developed in a completely independent way from human intelligence. In fact, in contrast to the mammalian brain, the avian brain does not have a cortex. There is no lamination and consequently not a columnar organization (Güntürkün, 2005; Kirsch et al., 2008). The lack of lamination originally led to believe that the avian brain consisted mainly of striatal tissue and with no pallium (Edinger, 2015). This view is now rejected (Jarvis et al., 2005; Reiner et al., 2004). The mammal prefrontal cortex is absent

in the avian brain. Instead, birds possess a large nidopallium caudolaterale (NCL). The NCL is believed to be the main structure for the integration of multimodal information and for the control of goal-directed behavior (Shanahan, Bingman, Shimizu, Wild, & Güntürkün, 2013). The connectivity of the NCL is highly comparable to the PFC: they are reciprocally connected with all secondary sensory and motor areas. They both are the major pallial target of dopaminergic projections and lesions to PFC and NCL have comparable effects on behavior (Kirsch et al., 2008). Both areas are highly innervated with dopaminergic fibers from the substantia nigra and ventral tegmental area (Divac, Mogensen, & Björklund, 1985; Wynne & Güntürkün, 1995), which terminate chiefly on excitatory synapses, activating D1-like receptors (Schnabel et al., 1997). The distribution of these receptors in the NCL is also in accordance with mammalian data (Durstewitz, Kröner, & Güntürkün, 1999; Herold et al., 2011). Moreover, other receptors (GABAergic, muscarinic, nicotinic, noradrenergic, serotonergic and glutamatergic) were found with a similar architecture (Herold et al., 2011).

In pigeons (Fig. 2A), NCL has been well characterized with many different behavioral/lesion (Mogensen & Divac, 1982, Wynne & Güntürkün, 1995), electrophysiological (Diekamp, Kalt, & Güntürkün, 2002; Kalenscher et al., 2005; Rose & Colombo, 2005), neurochemical (Divac et al., 1985; Waldmann & Güntürkün, 1993; Wynne & Güntürkün, 1995) and anatomical (Kröner & Güntürkün, 1999) studies. Activity in NCL reflects integrated information of the value of reward based on a combination of reward amount and reward delay (Dykes, Klarer, Porter, Rose, & Colombo, 2018; Kalenscher et al., 2005). Comparable to PFC neurons, NCL neurons categorize stimuli based on behavioral relevance (Kirsch et al., 2009). Neurons in the NCL maintained relevant stimulus information (Johnston, Anderson, & Colombo, 2017) only when the animals were instructed to maintain it and not when a stimulus was irrelevant (Rose & Colombo, 2005).

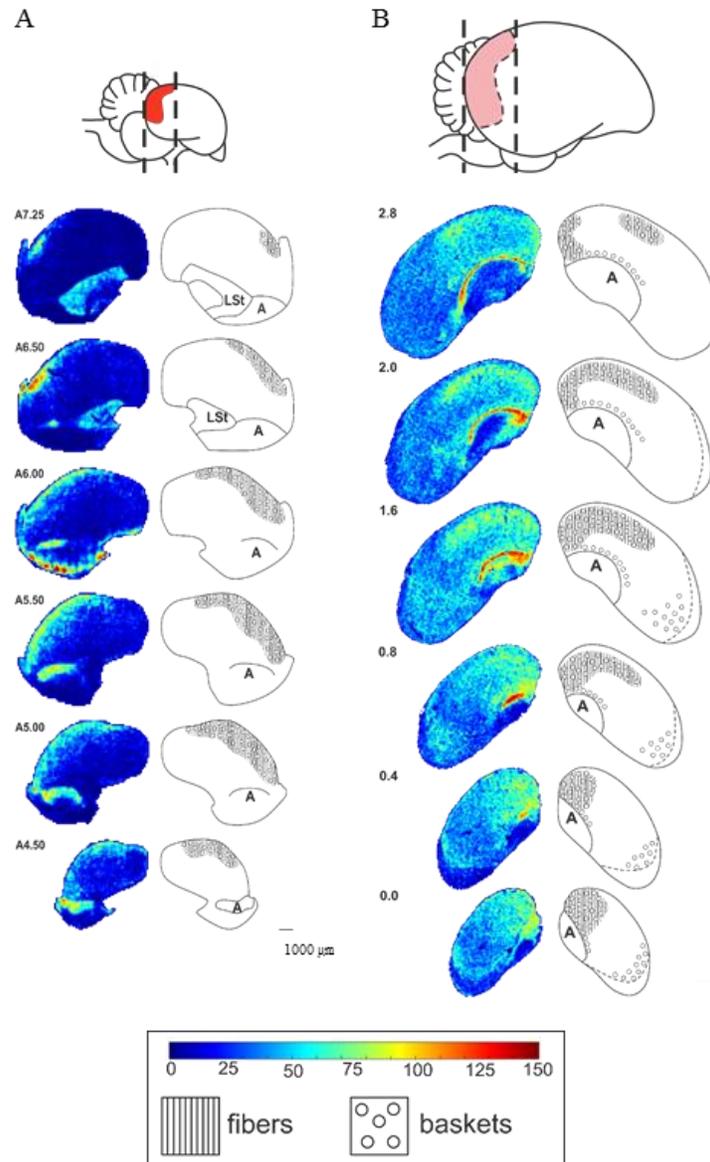


Figure 2. The Nidopallium Caudolaterale.

In the upper part a drawing of A) the pigeon brain and of B) the carrion crow brain with the nidopallium caudolaterale (NCL) highlighted, followed by schematic drawings of the frontal sections of the left hemisphere with the distribution of baskets consisting of fibers and non-basket type fibers. The pigeon sections are ranging from A7.25-A4.50 and the carrion crows sections from A2.80-A0.00. Scale bar indicates 1000 µm. Taken from von Eugen (2018).

On the contrary, in crows NCL is scarcely investigated. It was first identified in a study by Veit & Nieder (Veit & Nieder, 2013) who, following the method employed in pigeons (Waldmann & Güntürkün, 1993) executed a stain against tyrosine hydroxylase (TH), and defined the NCL as

the area with the highest T-fibers (*Corvus corone corone*, Veit & Nieder, 2013). In carrion crows' studies, they reported the NCL to be located as a semi-lunar area in the caudal telencephalon below the lateral ventricle. TH immunohistochemistry (IHC) has been executed in the zebra finch (Bottjer, 1993), Japanese quail (Bailhache & Balthazart, 1993), canary (Appeltants, Ball, & Balthazart, 2001), budgerigar (Roberts, Cookson, Heaton, Hall, & Brauth, 2001), chicken (Metzger, Jiang, Wang, & Braun, 1996; Moons, D'Hondt, Pijcke, & Vandesande, 1995; Schnabel et al., 1997) and carrion crows (Ditz & Nieder, 2015; Veit & Nieder, 2013). In contrast, from a recent immunohistochemical study with the aim to quantify and compare the relative volume of the NCL between pigeons and corvids species (Eurasian jay and carrion crow) a different picture emerges (Fig. 2B; von Eugen, 2017). Here, the area of highest innervation was found to be located more medial, midway between the lateral border and the arcopallium and arching in parallel to the arcopallium. A stain against myelin confirmed that this area also had a strong connectivity with the dorsal arcopallium, comparable to the dorsal arcopallial tract in the pigeon brain (von Eugen, 2017), underling the 'NCL-nature' of this area. Another recent IHC study confirmed the high density of both TH-fibers and TH-positive 'baskets' in several parts of the caudal nidopallium in house crows (*Corvus Splendens*), especially in the medial part of the NCL (mNCL) and in the ventrolateral part of the NCL (vLNCL), most commonly reported as the corvid NCL (Sen et al., 2019). In general, it appears the caudal nidopallium of the crow receives a much more widespread and varied TH-innervation compared to the pigeon brain (von Eugen, 2017; Sen et al., 2019), which complicates delineating one specific area as the "avian PFC".

The vLNCL has been already seen implicated in many electrophysiological studies (Nieder, 2017). The first single-unit recordings was established by Nieder and Veit in 2013 (Veit & Nieder, 2013). They showed the existence of rule-selective neurons from the vLNCL that could predict choice in carrion crow (Veit & Nieder, 2013). This is highly comparable to single-neuron activity of decision-making found in the PFC in monkeys (Nieder, 2017). Many vLNCL neurons represent basic visual features (Wagener, Loconsole, Ditz, & Nieder, 2018). The neuronal tuning of vLNCL neurons to different parameters allowed rapid change according to task demands (Moll & Nieder, 2015). This tuning flexibility is reminiscent of the responses of prefrontal neurons that can encode a variety of cognitive factors during delayed response tasks (Miller, 2000). The prefrontal neurons are known to dynamically adapt their tuning properties to different task demands, both at single neurons (Merten & Nieder, 2013; Rao, Rainer, & Miller, 1997) and at population level (Rainer,

Asaad, & Miller, 1998; Stokes et al., 2013). The vNCL neurons are not only sensitive to the encoding phase, but also they temporarily maintain visual information after the stimulus disappeared, during a brief delay (Veit et al., 2014). Those cells remained active during the short period of remembering like delay cells in the PFC. Prolonged activation of such cells ensured that important information could be stored and later accessed. Similar to the primates PFC, cognitive flexibility in corvids can depend on the capacity of the NCL to encode dynamically task relevant information.

AIM OF THE THESIS

In the present thesis, I investigate the presence of attention and control mechanisms involved in the allocation and reallocation of WM resources for the current task goal.

CHAPTER 1

The first chapter explores the cue effect in crows as attention and control mechanisms of WM. Attention can maximize WM capacity either prior to stimulus presentation (pre-cue), or even after stimuli have disappeared (retro-cue) through control mechanisms. In order to chart the presence of anticipatory and retrospective shifts of attention, crows perform a change detection task (Rensink, 2002). To summarize the action of attention and control mechanisms in WM at performance level, the task consists of three different conditions selected by the spatial cue-type (no-cue, pre-cue and retro-cue), at different memory loads. Importantly, this is the first time investigating the presence of a retro-cue effect in crows.

CHAPTER 2

In the second chapter, single-neuronal activity of attention over WM is recorded in crows performing a modified version of the same change-detection paradigm used in the previous experiment. To better understand the attentional modulation on the WM representations within multisensory areas, we record in the corvid vLNCL, the functional analogue of the mammalian PFC. Moreover, in view of the recent IHC findings, we record simultaneously also in the mNCL, to elucidate its implication in WM.

CHAPTER 3

In the third chapter, an executive control ability over WM in crows is discussed. Executive control must be recruited through a challenging WM task that includes information updating and monitoring (Smith & Jonides, 1999). Since its leading and flexible nature in cognition (Anderson & Reidy, 2012), the lack of an accurate executive control paradigm lies on the difficulties to incorporate more complex life-like challenges within performance measures (Chan, Shum, Touloupoulou, & Chen, 2008; Shallice & Burgess, 1991). To overcome these issues, we propose a novel

task that allows assessing a WM updating, modulation of representations and protection against interference (Baddeley, 1986; Logie, 2011; McCabe et al., 2010). The fulfillment of these cognitive abilities demands crows to activate all their WM resources over different reward magnitudes and spatial domains in a controlled and supervised way. The task will allow understanding crows' ability and limits in controlling the online information in their WM.

The aim is to understand the efficiency of WM in crows related to the attentional and executive control abilities. The success in the present WM tasks in the corvid model can help in the understanding of the constraints placed at behavioral level and help identifying the crucial neural features of attention and executive control in coordinating the memory resources. The evidence in support of a role for attention and executive control in corvids WM has not been settled, and it remains an open question whether they are an indispensable aspect of their advanced cognitive abilities. The assumption that crows possess attention and cognitive control in memory resources may explain their exquisite behaviors and helps to increase our understanding of the neural basis of cognition.

CHAPTER 1:

Crows show attention and control mechanisms over working memory.

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Abstract

Working memory (WM) has a limited capacity and this limit is comparable in crows and primates.

It is well established, that humans can use attention to maximize WM by selecting only relevant stimuli for maintenance. Interestingly, such attention-cues are effective not only before but also after the presentation of to-be-remembered stimuli, highlighting control mechanisms beyond sensory selection. Here we explore if crows are also capable of these forms of control over working memory. Two crows (*Corvus corone*) were trained on a change detection task. We used one pre- and retro-cues to direct attention to a spatial location in a two, four or six stimulus array, in combination with no-cue conditions. We found that both pre- and retro-cues enhanced performance and abolished the load effects for accuracy and capacity limits. When no cue was given, the crows showed a memory load-effect, a decrease in performance with increasing number of stimuli.

These results show that crows, like humans can utilize attentional cues to efficiently direct visual attention to critical stimuli. Importantly, the crows can also utilize cues to improve working memory capacity even after the stimuli are already held in WM and no longer visually accessible. This strongly implies that crows can engage in control over information held in working memory.

Keywords: cue effect, retro-cue, crows, attention, executive control, working memory.

Introduction

Working memory (WM) refers to the ability to memorize information over short periods and, importantly, to process this information. This makes WM a core component of cognition that is critical for decision making, planning, goal directed behavior and many other cognitive abilities (Baddeley & Hitch, 1974; Miller et al., 1960). It is well established that WM is not a passive storage but that it requires active maintenance of information (Ricker & Cowan, 2010). Consequentially, WM is not only vulnerable to distraction but also limited in duration and in capacity (Cowan, 2012). Estimates of the capacity of WM suggest that only about four items can be maintained simultaneously (Cowan, 2001; Irwin & Andrews, 1996; Luck & Vogel, 2013; Sperling, 1960; Vogel, Woodman, & Luck, 2001). This capacity-limitation is a critical bottleneck of cognition and has recently been coined the ‘bandwidth of cognition’ (Cowan, 2010; Miller & Buschman, 2015).

In the light of these limitations, it is evident that WM must rely on effective top-down control (Awh et al., 2006). This control can occur in different ways. Attention can act as a ‘gatekeeper’ that prioritizes the encoding of relevant sensory stimuli and filters out irrelevant information (Awh et al., 2006; Broadbent, 1958; Carrasco, 2011; Ku, 2018; Yantis, 2008). While this mechanism is highly effective, it requires prior knowledge about the relevance of upcoming sensory events. Therefore, the system also needs the ability to control the maintenance of information that is already held in WM. In humans, it is well established that attention is used to gate stimuli for WM and that there is executive control over information maintained in WM. Pioneering work from Posner and Cohen (1984) demonstrated that visual cues facilitate target detection if a location is cued prior to the presentation of the target. Likewise, such ‘pre-cues’ facilitate the retrieval of visual stimuli following a period of WM maintenance. This illustrates the importance of attentional ‘gatekeeping’ for visual WM (Pertzov et al., 2013). Most interestingly, cue-stimuli are effective also *after* stimulus-presentation. Like pre-cues, such ‘retro-cues’ increase the retention of cued material but to a lesser extent (Astle et al., 2012; Berryhill et al., 2012; Griffin & Nobre, 2003; Landman et al., 2003; Lepsien et al., 2005; Makovski, 2012; Makovski & Jiang, 2007; Sligte et al., 2008, 2009). Since this effect cannot be driven by sensory gate-keeping it must rely on some form of control mechanism that drive the focus of attention over WM information.

Humans studies have shown that pre- and retro-cues improve performance, increase detection rates and decrease reaction times (Astle et al., 2012; Berryhill et al., 2012; Carrasco, 2011; Griffin &

Nobre, 2003; Lepsien et al., 2005; Matsukura, Luck, & Vecera, 2007; Posner, 1980; Sligte et al., 2009).

The physiological mechanism that underlies WM, active stimulus maintenance, is largely comparable between different species (Courtney, Petit, Haxby, & Ungerleider, 1998; Cowen & McNaughton, 2007; Diekamp et al., 2002; Funahashi, 2017; Funahashi & Kubota, 1994; Fuster, 1973; Joaquín M. Fuster, 2001; Goldman-Rakic, 1996; Kubota & Niki, 1971; Postle, Berger, Taich, & D’Esposito, 2000; Rose & Colombo, 2005; Tsutsui, Oyama, Nakamura, & Iijima, 2016; Veit & Nieder, 2013). Likewise, attentional mechanisms are not restricted to humans since monkeys (Cook & Maunsell, 2002; Eckstein et al., 2013; Maunsell & Cook, 2002), rats (Bushnell & Rice, 1999; Marote & Xavier, 2011), chickens (Sridharan, Ramamurthy, Schwarz, & Knudsen, 2014) and pigeons (Eckstein et al., 2013; Maunsell & Cook, 2002; Shimp & Friedrich, 1993) also benefit from pre-cues. All those species are able to use predictive cues but, on the other hand, it is poorly understood if animals are able to gate WM using attention or if they are able to control WM-maintenance since the pre-cue effect was never tested on WM capacity in animal research. Moreover, the effects were limited to test only individual parameters like percent correct (Eckstein et al., 2013), the latency of responses (Marote & Xavier, 2011; Shimp & Friedrich, 1993), and the effect could have been dependent on features of the stimuli (e.g. the contrast-ratio (Sridharan et al., 2014)). It remains unclear whether animal WM includes a similar effect with the retro-cues. To the best of our knowledge, only one experiment examined if animals can use retro-cues to improve WM (Brady & Hampton, 2018). In that study, monkeys were presented with arrays of two or three visual stimuli and a retro-cue that indicated relevant stimuli after stimulus presentation. The cue was beneficial for accuracy and reaction time. Interestingly, the monkeys only benefited from the cue at a load of two stimuli but not at a load of three stimuli. The authors concluded that a memory load of three images could result in “insufficient memory strength” for the retro-cue to have an effect (Brady & Hampton, 2018). A different protocol, direct forgetting, was used with a similar aim – to investigate the executive control over WM in animals (Kendrick et al., 1981; Rose & Colombo, 2005; Zentall & Smith, 2016). In directed forgetting paradigms, cues instruct the subjects if a memorized stimulus will later become relevant or if it can be forgotten. While such ‘forget-cues’ result in a dramatic decline in recognition, it is not fully resolved if this reflects executive control or if the results can be explained by simpler mechanisms such as motivational differences (Browning, Overmier, & Colombo, 2011). This is a problematic notion since the cues to remember or to forget imply in most instances the

presence or absence of a reward at the end of the trial. Another example, sharing a rule structure principle, was in Veit and Nieder (2013) in which crows were trained to switch between two general rules in a delayed match/nonmatch-to-sample task. The task, focused on neuronal analysis, did not enlarge from one stimulus retrieval.

A wealth of other experiments demonstrated that corvid birds tap into different executive functions (Emery and Clayton, 2004; Balakhonov & Rose, 2017). For instance, corvids manufacture and use tools (Weir, 2002), exhibit episodic-like memory (Emery & Clayton, 2004) and master elaborate tests of object permanence (Hoffmann, Rüttler, & Nieder, 2011) including problem-solving abilities (Auersperg et al., 2011; Kabadayi & Osvath, 2017; Logan et al., 2014; Taylor, Hunt, Medina, & Gray, 2009; Taylor et al., 2011). These results could imply that corvids are able to direct attention to relevant stimuli and that they can control their cognitive resources. However, this was never demonstrated directly. We recently showed that crows have a high WM-capacity that is comparable to the capacity of rhesus monkeys in a virtually identical paradigm (Balakhonov & Rose, 2017; Buschman et al., 2011). Here, we modified this paradigm and included trials with pre- or retro-cues while the animals performed either below, at, or above their WM-capacity. In this way, we test whether crows have attention and control mechanisms that efficiently drive WM resources on relevant information. The design of the task meant to fill the gap of the animal literature in the cue effect, offering all the behavioral measures of memory performance: proportions of correct responses, accuracy, capacity measures and reaction time. This allowed to study how far crows are able to use attention to gate WM towards the maintenance of relevant stimuli. Importantly, it also allowed to test if crows can control WM and select among already maintained stimuli through shifting of attention on the relevant one. Thus, if we observe retro-cue effects, this would indicate a previously unknown control mechanisms in crows.

Materials and Methods

Subjects

Two hand raised male carrion crows (*Corvus corone*), 3 years of age, with baseline weights of 505 and 500 g, were used. The crows were housed in a social group of 5 birds in an indoor aviary with a controlled 12 hours day/night cycle. When not in experiments, the birds were given ad libitum

access to water, grit and food (Versele Laga Nutribird F16, BeoSoft, occasionally nuts, fruit, chicks and mealworms). During experiments the crows were maintained on a controlled food protocol with free access to water and grit. Food-pellets (Nutribird F16, Versele-Laga, Germany) and mealworms were used as reward. The animals' body weight was controlled daily and maintained between 85 and 95 %. All preparations and procedures were performed according to the principles of the care and use of laboratory-animals adopted by the German Animal Welfare Law for the prevention of cruelty to animals and were conducted after approval by the LANUV (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen).

Experimental setup

The setup consisted of a chamber (50 cm (width) x 50.5 cm (depth) x 77.5 cm (height), equipped with a remote monitoring camera (Sygonix, Taiwan), a 22" touchscreen-monitor (ELO 2200L APR, Elo Touch Solutions, Inc) and a custom-made automatic pellet feeder (plans available: www.jonasrose.net). The bird was placed on a wooden perch in front of the touchscreen such that the maximum distance from the bird's eye to the screen was 7 cm. The animal's head position and rotation were tracked in the horizontal and vertical plane, using two computer-vision cameras (Chameleon3, Point Grey Research Inc., Richmond, BC, Canada). For tracking, a custom 3d-printed reflector was mounted on a lightweight surgically implanted head-post and removed after each experimental session. The frame rate of the cameras were 75 Hz and data was smoothed by integrating over 2 frames using custom code on a control PC. All experiments were controlled by custom programs in Matlab (Mathworks inc. Natick, MA USA) using the Biopsychology (J. Rose, T. Otto, L. Dittrich, 2008) and Psychophysics toolboxes (Brainard, 1997). Digital input and output of the control PC was handled by a microcontroller (ODROID C1, Hardkernel co. Ltd) running custom software (available: www.jonasrose.net) connected through gigabit network. This allowed for flexible and temporally precise IO-communication.

Behavioral protocol

The crows were trained on a change detection task (Fig. 3). Following the training period, each bird was tested daily to collect data over ten days. During experimental sessions, the animals were offered access to water during brief breaks.

Each trial started with an inter-trial interval (4000 ms) after which the crows were presented with a red dot in the center of the screen (maximal 5000 ms) that served as a cue to start the trial. The trial started when the crows centered their heads and looked straight at the center of the screen (± 2 cm horizontal or vertical displacement, $\pm 17^\circ$ horizontal or vertical head-rotation). This head position had to be maintained until the end of the trial or the trial was aborted. For a not started or aborted trial crows received negative feedback in the form of a timeout (9000 ms) and a brief white illumination of the screen. On all trials, the birds were presented with a sample-array (400 ms) that consisted of 2, 4 or 6 colored squares. At the end of each trial, the sample-array re-appeared as comparison-array. On half the trials, the comparison-array was identical to the sample-array, on the other half one color was exchanged. Following the presentation of the comparison -array (400 ms) all colors turned gray and one additional grey square appeared in the center of the screen. Crows were trained to indicate if the sample- and comparison-arrays were identical (a choice had to be made within 4000 ms). If there was no change, birds had to peck the new square in the center. If there was a change, crows had to peck on any of the peripheral squares. In order to perform this paradigm successfully, the crows had to memorize the sample-array on each trail and to compare it to the comparison -array. If the animals made a correct response, a single food-pellet was delivered as reward to the automated feeding-trough, which was illuminated during reward-delivery (2000 ms). An incorrect response or a response-omission resulted in negative feedback, a brief white illumination of the screen and a time-out (9000 ms).

Each training session consisted of three conditions: a no-cue condition, a pre-cue condition and a retro-cue cue condition. While the overall trial-length of all three conditions was matched, the trails differed in the delays before or after the presentation of the sample-array. In the cue conditions, a white circle appeared for 200 ms either in the delay before the sample-array (pre-cue) or in the delay before the comparison -array (retro-cue). The cues instructed the animals that, if there was a color-change on the trial, it would occur on the cued-location. Therefore, the cues could be either be used to direct attention to a specific spatial location during viewing of the sample-array (pre-cue) or to select one color from WM (retro-cue). On no-cue trials a sample-array-size of 2, 4 or 6 colors was used while on pre- and retro-cue trails only arrays of size 4 and 6 were used.

The design of the stimuli was based on the protocol by Buschman et al. (Buschman et al., 2011). On each trial, two, four or six colors were presented at fixed screen locations. For every day, random color-combinations were chosen from a set of 14 colors such that six pairs, one for each stimulus-

location were chosen on a given day. Thus, on each training day, one random pair of colors was fixed to each of the six stimulus locations. The order of presentation of the colors within a pair was randomized and balanced across conditions. The target location for cued and un-cued conditions, the total number of stimuli in the array and the number of stimuli on the target hemifield were randomized such that all conditions had equal likelihood on a given trial. Color-stimuli were square, 10 degrees of visual angle (DVA) on either side and placed either on the horizontal meridian of the screen or 45.8 DVA above/ below the meridian at a distance from the center of 54 and 55.4 DVA (center of the stimulus) respectively (Balakhonov & Rose, 2017) (Fig. 3). The cue stimuli were white thin transparent circles of 11 DVA, positioned on the exact location of the color-stimuli to cue. The maximal binocular overlap for carrion crows is around 37.6 DVA (Troscianko, von Bayern, Chappell, Rutz, & Martin, 2012); thus all color-stimuli and cues were placed outside the binocular area, taking into account head-movement, head-rotation and eye movement.

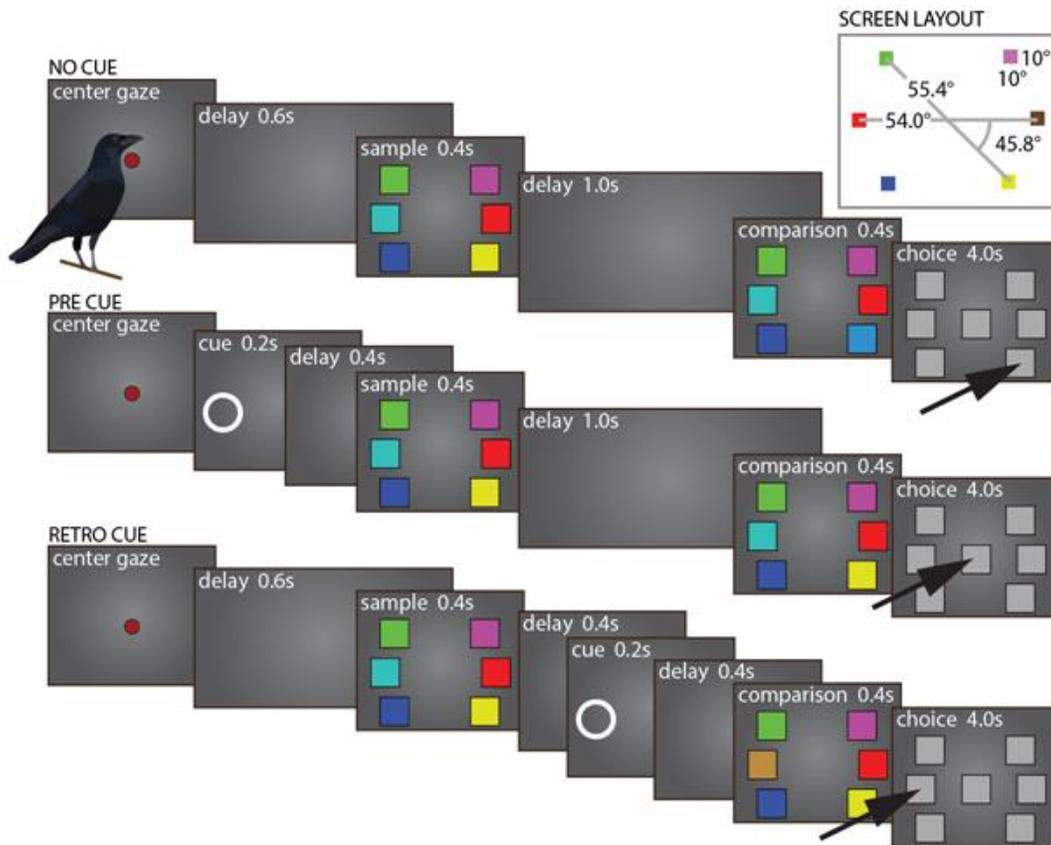


Figure 3. Behavioral protocol: the change detection task.

The crow had to hold his head static and look straight at the center of the screen to start the trial and during the ongoing trial. Each training session had a no-cue, a pre-cue (prior sample onset) and a retro-cue condition (after sample offset). In the no-cue condition, after a short delay of 0.6 s, an array of 2, 4 or 6 colored squares appeared for 0.2s and had to be maintained in WM for 1 s. In the pre or retro-cue conditions (only with 4 and 6-colors), a thin white circle appeared for 200 s to target a specific location. Preceding and following a retro-cue there was a brief delay of 0.4 ms. At the end of each condition, the sample array re-appeared identical or with one color changed (comparison-array). The comparison-array turned gray after 0.4 s in the choice period: a correct response was a peck on the centered square available (no-change), or any peck on the peripheral squares (change). In the top right, the size and position of the stimuli in degrees of visual angle (DVA).

Surgery

All surgeries were performed under aseptic procedures. For the head tracking system, a light-weight head-post was chronically implanted to position a small silver colored reflector during behavioral experiments. Before surgery, crows were induced by ketamine (50mg / kg) and xylazine (5 mg / kg). Once deeply anaesthetized, crows were placed in a stereotaxic frame. Few feathers were plucked over the base of the beak exposing skin for a small incision to retract the skin. A small

opening was drilled in the surface of the bone in order to expose the *trabeculae* to which the head-post was attached with dental acrylic. The wound-margins were sutured. Following the administration of analgesia (morphasol, 3 ml / kg) the crow was placed in a recovery-cage until fully recovered.

Data analysis

Data was collected and analysed with Matlab (Mathworks inc. Natick, MA) using custom code and the statistics toolbox. Data analyses were based on attempted trials, from the fixation acquired on the starting dot to a correct or an incorrect response, excluding therefore gaze-breaks trials. All the behavioral measures, the effects of cue type and number of stimuli on performance, gaze-breaks, reaction time, sensitivity score for change/no-change discrimination (d' score) (Green & Swets, 1966) and memory-capacity measurement (Pashler-K, Rouder et al., 2011) were assessed with 2-way ANOVA with memory load and cue-type as independent variables across days, followed by Tukey-Kramer Honest Significantly Different (HSD) post-hoc analysis. ANOVAs were conducted for each crow independently.

Results

The crows were previously trained on a change localization paradigm (Balakhonov & Rose, 2017) and then retrained for approximately 4 months. During this time, they learned the cued change detection paradigm reported here. Following the training period, the animals were tested for ten days. Both birds, (FRN, JRO) performed 850 trials daily with an overall performance that was well above chance (FRN: mean \pm SEM 76.54 % \pm 0.86, JRO: 74.15 % \pm 0.89).

As previously reported for a change-localization paradigm (Balakhonov & Rose, 2017), performance declined significantly with an increase in memory load concerning the no-cue condition (2, 4 and 6-colors) (Fig.4A) (one-way ANOVA FRN: $F(2,27) = 49.00$, $p < .001$; JRO: $F(2,27) = 18.47$, $p < .001$; post-hoc test: 2-colors FRN: $M = 85.45$ % $SD = 1.58$; JRO: $M = 77.30$ % $SD = 1.87$; 4-colors FRN: $M = 69.77$ % $SD = 1.58$ JRO: $M = 67.19$ % $SD = 1.87$; 6-colors FRN: $M = 63.95$ $SD = 1.58$ JRO: $M = 61.36$ $SD = 1.87$). This drop in performance was not significant in the pre-cue condition (4 and 6 colors) (one-way ANOVA FRN: $F(1,18) = 0.22$, $p = .64$; JRO: $F(1,18) = 0.01$, p

= .904). In the retro-cue condition it reached significance for one of the two animals (4 or 6 colors) (one-way ANOVA FRN: $F(1,18) = 1.33$, $p = .26$; JRO: $F(1,18) = 5.952$, $p = .025$).

A two-way ANOVA tested the effect of the cues and memory load on performance.

Both birds benefited from the presence of cues: both pre and retro-cue significantly increased the performance compared to the no-cue condition (Fig. 4A; ANOVA FRN: $F(2,30) = 34.62$, $p < .001$; JRO: $F(2,30) = 60.50$, $p < .001$; post-hoc test: no-cue: FRN $M = 66.8$ $SD = 1.21$; JRO $M = 64.2$ $SD = 1.09$; pre-cue FRN $M = 81.0$ $SD = 1.09$; JRO: $M = 81.3$ $SD = 1.09$; retro-cue FRN: $M = 75.5$ $SD = 1.09$; JRO $M = 71.5$ $SD = 1.09$) with a memory load effect only in JRO (ANOVA FRN: $F(9,30) = 1.90$, $p = .09$; JRO: $F(9,30) = 4.55$, $p < .001$) but there was no interaction between both factors (ANOVA FRN: $F(18,30) = 1.08$, $p = .40$; JRO: $F(18,30) = 1.53$, $p = .14$).

We used the sensitivity score for change/no-change discrimination (d' score) (Green & Swets, 1966; Macmillan and Creelman's 1991). The d' score was calculated using the following equation:

$$d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$$

Hit rate was defined as the conditional probability that the participants responded “change-present” given that the change was presented, and the false-alarm rate was defined as the conditional probability that the participants responded “change-present” when the change was absent.

Along with the performance, the d' significantly decreased on the memory load in the no-cue condition (Fig.4B; one-way ANOVA FRN: $F(2,27) = 23.30$, $p < .001$; JRO $F(2,27) = 6.741$, $p < .001$). Both birds were more accurate to detect the change in the cue conditions compared to the no-cue condition (Fig.3 ANOVA FRN: $F(2,30) = 25.34$, $p < .001$; JRO: $F(2,30) = 31.90$, $p < .001$; post-hoc test: no-cue: FRN $M = 1.06$ $SD = 0.08$; JRO $M = 0.90$ $SD = 0.12$; pre-cue FRN $M = 1.93$ $SD = 0.08$; JRO $M = 2.03$ $SD = 0.12$; retro-cue FRN: $M = 1.47$ $SD = 0.08$; JRO $M = 2.25$ $SD = 0.12$) with a memory load effect only in JRO (ANOVA FRN: $F(9,30) = 1.63$, $p = .14$; JRO: $F(9,30) = 3.01$, $p = .01$) but there is no interaction between both factors (ANOVA FRN: $F(18,30) = 1.02$, $p = .45$; JRO: $F(18,30) = 1.77$, $p = .08$).

The WM-capacity (Pashler-K measure, Rouder et al., 2011) was calculated using the following equation:

$$\hat{k}_p = N \left(\frac{\hat{h} - \hat{f}}{1 - \hat{f}} \right)$$

The capacity K did not differentiate between the no-cue conditions by the WM load (Fig. 4C; one-way ANOVA FRN: $F(2,27) = 2.65$, $p = .08$; JRO: $F(2,27) = 1.401$, $p = .26$).

Both crows show a higher WM capacity on the cue conditions when comparing with the no-cue condition, demonstrating an increase in information about the stimulus-array (Fig.4C; ANOVA FRN: $F(2,30) = 20.12$, $p < .001$; JRO: $F(2,30) = 23.54$, $p < .001$; post-hoc test: no-cue: FRN $M = 0.75$ $SD = 0.07$; JRO $M = 0.62$ $SD = 0.07$; pre-cue FRN $M = 1.46$ $SD = 0.07$; JRO $M = 1.39$ $SD = 0.07$; retro-cue FRN: $M = 1.06$ $SD = 0.07$; JRO $M = 0.97$ $SD = 0.07$) with a memory load effect only in JRO (ANOVA FRN: $F(9,30) = 1.43$, $p = .21$; JRO: $F(9,30) = 2.80$, $p = .01$), but there is no interaction between both factors (ANOVA FRN: $F(18,30) = 0.64$, $p < .83$; JRO: $F(18,30) = 1.61$, $p = .11$).

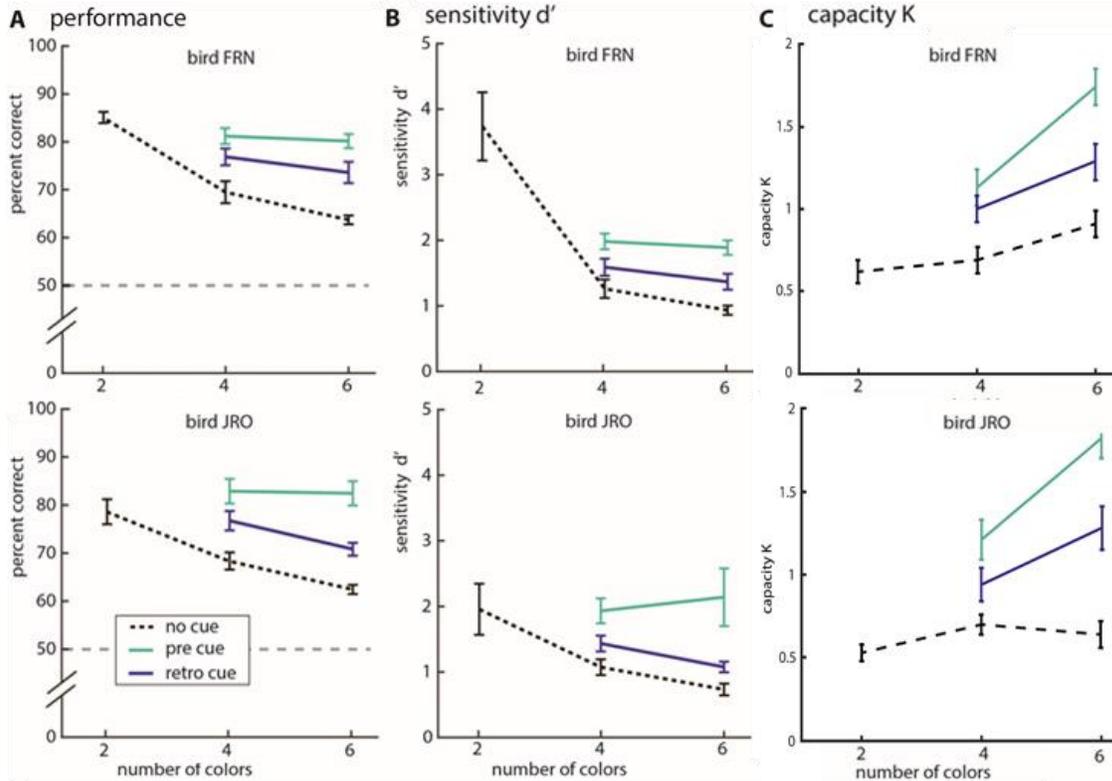


Figure 4. The cue effect.

A) Behavioral performance (percent correct) of both crows as a function of task conditions (4 items FRN: no-cue: mean \pm SEM=69.77 \pm 2.30; pre-cue: 81.54 \pm 5.28; retro-cue: 77.19 \pm 5.57; JRO no-cue: 67.19 \pm 1.781; pre-cue: 81.51 \pm 8.033; retro-cue: 75.46 \pm 6.290; 6 items FRN: no-cue: 63.95 \pm 0.94; pre-cue: 80.49 \pm 4.68; retro-cue: 73.90 \pm 7.05; JRO no-cue: 61.36 \pm 0.945; pre-cue: 81.08 \pm 7.868; retro-cue: 69.62 \pm 4.220); chance level is 50 %. B) The sensitivity d' as a function of task conditions (4 items: FRN: no-cue: 1.26 \pm 0.14; pre-cue: 1.98 \pm 0.12; retro-cue: 1.58 \pm 0.13; JRO no-cue: 1.072 \pm 0.125; pre-cue: 1.931 \pm 0.194; retro-cue: 1.433 \pm 0.127; 6-colors: FRN: no-cue: 0.93 \pm 0.07; pre-cue: 1.88 \pm 0.11; retro-cue: 1.36 \pm 0.12; JRO no-cue: 0.732 \pm 0.092; pre-cue: 2.140 \pm 0.449; retro-cue: 1.075 \pm 0.089). C) The WM capacity K as function of task conditions: (4-colors FRN: no-cue: 0.69 \pm 0.08; pre-cue: 1.13 \pm 0.11; retro-cue: 1.00 \pm 0.08; JRO no-cue: 0.70 \pm 0.06; pre-cue: 1.21 \pm 0.12; retro-cue: 0.94 \pm 0.1; 6-colors FRN: no-cue: 0.91 \pm 0.08; pre-cue: 1.74 \pm 0.11; retro-cue: 1.29 \pm 0.13; JRO no-cue: 0.64 \pm 0.08; pre-cue: 1.82 \pm 0.12; retro-cue: 1.28 \pm 0.08). Error bars are SEM.

The reaction times increased on incorrect compared to correct choices, but only for FRN (one-way ANOVA FRN: $F(1,18) = 6.98$, $p < .001$; post-hoc test FRN: corr: $M = 0.36$ s $SD = 0.14$; incorr: $M = 0.39$ s $SD = 0.12$; JRO: $F(1,18) = 2.61$, $p = .12$). Both birds had a similar reaction time of correct responses between the conditions (Fig. 5A; ANOVA FRN: $F(2,30) = 0.08$, $p = .91$; JRO: $F(2,30) = 0.01$, $p = .98$). Along with the performance, both birds significantly increased their response time increasing the number of items to remember (ANOVA FRN: $F(2,30) = 21.35$, $p < .001$; JRO: $F(2,30)$

= 3.06, $p = .01$: post-hoc test: 4-colors FRN: 0.30 s SD = 0.16; JRO M = 0.31 s SD = 0.08; 6-colors FRN: M = 0.39 s SD = 0.16; JRO M = 0.34 s SD = 0.08) with no interaction between the 2 factors (ANOVA FRN: $F(18,30) = 1.28$, $p = .26$; JRO: $F(18,30) = .89$, $p < .58$).

To determine whether there were any spatial response biases, we analysed the performance by location. JRO showed a higher percent correct on location 1 while FRN, instead, showed a significant difference for location 6 at the expense of a lower performance (Fig. 5D; ANOVA FRN: $F(5,54) = 16.86$, $p < .001$ and post-hoc: location 6: M = 51.75 % SD = 3.53; JRO: $F(5,54) = 3.51$, $p = .008$ post-hoc: location 1: M = 88.02 % SD = 4.53). Since the stimuli were presented randomly at six locations, this does, however, not explain the effects of pre- or retro-cues.

A head-tracking system controlled the gaze-direction of the crows, to ensure the fixation position during stimulus presentation. Tracking allowed to prevent any strategies overcoming the location to choose (e.g. positioning their head on the stimulus location to remember). Comparing at each memory load, the gaze-breaks rate in no-cue trial was significantly lower (Fig. 5B; ANOVA FRN: $F(2,30) = 34.85$, $p < .001$; JRO: $F(2,30) = 13.12$, $p < .001$; post-hoc test: FRN: M = 11.49 % SD = 0.53; JRO M = 13.74 % SD = 0.42).

The omission rate at the choice was extremely low, covering only the 0.31 % in FRN and the 0.25 % in JRO of the total responses (Fig. 5C), underling the full engagement of the crow at each trial.

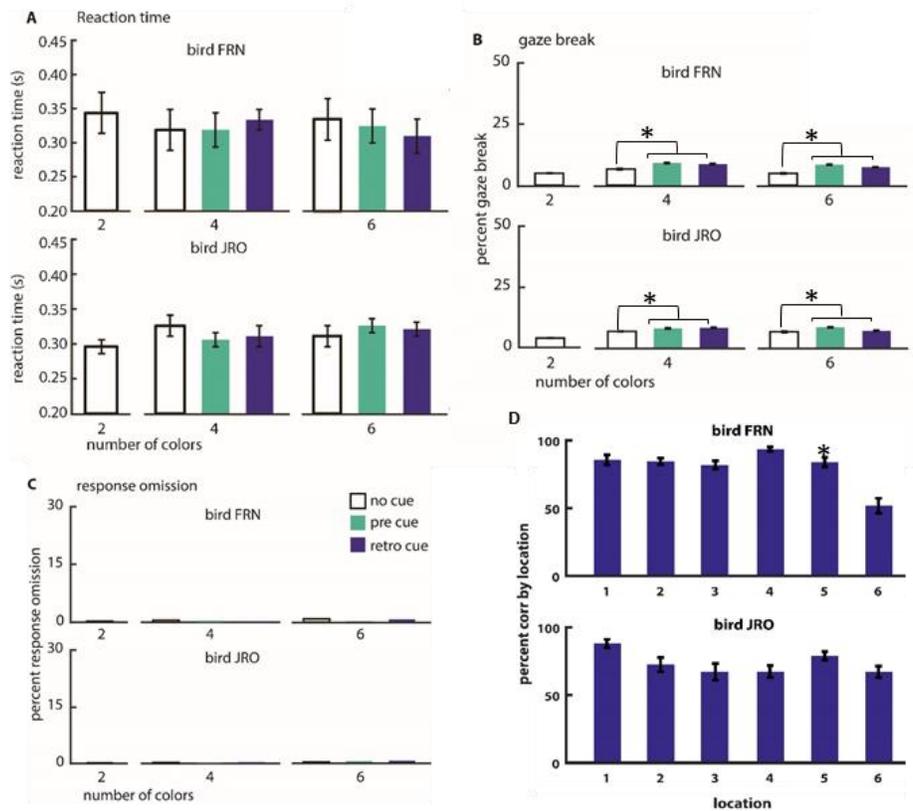


Figure 5. Reaction time and behavioral bias.

A) Reaction time of both crows on correct trials as a function of task conditions (FRN: no-cue: $0.36 \text{ s} \pm 0.05$; pre-cue: $0.35 \text{ s} \pm 0.05$; retro-cue: $0.34 \text{ s} \pm 0.05$; JRO no-cue: $0.32 \text{ s} \pm 0.02$; pre-cue: $0.33 \text{ s} \pm 0.02$; retro-cue: $0.33 \text{ s} \pm 0.01$). B) Percent of gaze-breaks of both crows on started trials as a function of task conditions (4-colors FRN: no-cue: $13.22 \% \pm 0.64$; pre-cue: $18.27 \% \pm 0.45$; retro-cue: $17.36 \% \pm 0.57$; JRO no-cue: $13.90 \% \pm 0.32$; pre-cue: $16.32 \% \pm 0.51$; retro-cue: $16.84 \% \pm 0.51$; 6-colors FRN: no-cue: $9.75 \% \pm 0.48$; pre-cue: $16.78 \% \pm 0.43$; retro-cue: $14.74 \% \pm 0.31$; JRO no-cue: $13.57 \% \pm 0.68$; pre-cue: $17.22 \% \pm 0.41$; retro-cue: $14.38 \% \pm 0.51$). C) Percent of omission rate (the lack of response in the choice) as a function of task conditions (FRN: no-cue: $0.46 \% \pm 0.132$; pre-cue: $0.25 \% \pm 0.03$; retro-cue: $0.45 \% \pm 0.13$; JRO no-cue: $0.20 \% \pm 0.07$; pre-cue: $0.35 \% \pm 0.13$; retro-cue: $0.50 \% \pm 0.10$). D) The percent correct as a function of stimuli locations. Error-bars are SEM.

Discussion

In this study, we characterized the presence or absence of a cue effect in crows at different WM loads. We found that crows, like humans and monkeys, can use spatial attentional cues to efficiently direct their attention to perceptual stimuli (pre-cue). Importantly, we demonstrate the

presence of control mechanisms directed to internal representations of stimuli held in WM (retro-cue). The animals were able to improve their memory accuracy and capacity when the stimuli were no longer visible on the screen but held in WM. By restraining their attention and control the accessibility of the relevant information, crows mitigate the WM capacity.

Consistent with previous studies in humans (Griffin & Nobre, 2003; Nobre, Griffin, & Rao, 2008), our results show that recall was more accurate for cue compared to no-cue conditions. For each crow, we analysed the typical behavioral measures to test the presence of a cue effect: percent correct, accuracy d' , memory capacity K and reaction time.

For both crows, pre- and retro-cues enhanced percent correct, accuracy d' and memory capacity K compared to no-cue conditions. Pre-cue conditions, compare to no-cue and retro-cue conditions, dramatically increased the performance, independently of the memory load. Like humans (Carrasco, 2011; Castiello & Umiltà, 1990; Posner & Petersen, 1990), crows use pre-cues to facilitate their WM during the task. The pre-allocation of their attention to the relevant stimulus' location yields the performance indistinguishable from no-cue 2-items condition. The accuracy and the capacity K on pre-cue conditions confirmed an optimal use in precisely detecting the change without increasing the false alarms and exceeding their capacity.

Notably, a similar effect was observed with the retro-cue condition. Compare to no-cue, retro-cue conditions increased performance and they were more accurate to detect the change without over-running into false alarms. Furthermore, the retro-cue conditions improved WM capacity compared to the no-cue conditions.

The retro-cue benefits seen in this task suggest that crows can exert control over the memory resources and shift the focus of attention within WM in a similar way to humans (Astable et al., 2012; Berryhill et al., 2012; Carrasco, 2011, 2011; Castiello & Umiltà, 1990, 1990; Griffin & Nobre, 2003; Landman et al., 2003; Lepsien et al., 2005; Makovski, 2012, 2012; Makovski & Jiang, 2007; Rerko et al., 2014; Sligte et al., 2008, 2009; Souza & Oberauer, 2016). Interestingly, the retro-cue effect in crows is comparable with humans' but not with monkeys'. Crows reveal an easier accessibility and control of WM resources, demonstrating a retro-cue effect at higher cognitive loads that surpass the monkeys limit of 2-items (Brady & Hampton, 2018).

Although the animal research on the retro-cue is far from a comparative solution, the human literature continued the research on this effect in WM. With a retro-cue, the access to the information appear to be different from a pre-cue because the encoding of the sample stimulus is not affected.

The stimuli information is already hold in WM, in the process of maintenance. It is here that the retro-cue acts as sensorial input at the to be tested location which changes stimuli accessibility based on behavioral demands.

A variety of explanations concerning the mechanisms of the retro-cue benefit has been suggested. Souza and Oberauer (2016) provided an overview of the different hypotheses and described that a retro-cued item could be protected from time-decay and from perceptual interferences. The retro-cue stabilizes the information of the selected stimulus and helps the recall in the comparison-array making the rest of the stimuli irrelevant. Moreover, the retro-cue could also remove the other items in WM and strengthen its prioritization. Therefore, it is possible that a cued item is strengthened and that non-cued items are removed at the same time (Rerko et al., 2014; Souza & Oberauer, 2016; Ye, Hu, Ristaniemi, Gendron, & Liu, 2016). These explanations may not find a targeted solution in our experiment, due to the use of the same cue reliability, same retention interval and same duration of stimulus-array, but our findings remark that the pre- and retro-cue effects are extremely comparable in all the behavioral measures. Even if the pre-cue improvements are more vigorous, both cues are minimizing the performance deficits induced by an increased number of items to remember. The higher K values of cues' conditions suggest that the animals can hold and extract more information from WM compared to no-cue conditions. This hints at the possibility that the same attentional mechanisms are involved in the selection and prioritization of the information in the encoding and maintenance of WM information (Souza & Oberauer, 2016).

Nevertheless, the comparability between both cue effects in this task remains also in the reaction time effect, which stays unchanged between the conditions. The birds were allowed to respond only 400 ms after the onset of the test-array, a sufficient time to encode and process the stimuli information and make a decision (Veit & Nieder, 2013).

In most of the tasks used in previous studies, the cue effect has not found an exhaustive behavioral analysis yet (Kendrick et al., 1981; Roper, Kaiser, & Zentall, 1995; Rose & Colombo, 2005; Shimp & Friedrich, 1993; Sridharan et al., 2014; Veit & Nieder, 2013). In the present task, each condition has the same retention interval and the same reward, avoiding motivational differences, as previously reported (Roper et al., 1995). The present change detection task allows an equally inclusive access to each behavioral cue effect and a detailed investigation of all the different behavioral measures for attention and control in WM. Behavioral and neurophysiological studies in animals have not yet allowed dissociating the effect of no-, pre- and retro-cue conditions during a WM

task under challenging memory loads. Thanks to its versatility, this paradigm can be modified easily in order to address attention and control efficiency in human and non-human models.

The corvid WM system possess mechanisms that efficiently control anticipatory and retrospective shifts of attention over information held in WM, which allows them to overcome their limited capacity. The robust cue-effect seen here provides a direct evidence that in crows, like in humans, attention is not limited in the encoding as passive filter for WM but also in the maintenance of the information. The action of attention is efficiently controlled and directed in the internal representation to manage the accessibility of relevant information.

While a different brain structure adopted attention and control mechanisms similar to humans, *In vivo* electrophysiology in behaving crows could allow rapid assessment of the conduction properties of the attentional control on the different stages of WM at a neuronal level.

CHAPTER 2:

Neural correlates of attention over working memory in the medial and the ventrolateral nidopallium caudolaterale.

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Abstract

Working memory (WM) is the neural system for short-term maintenance and manipulation of information with a limited capacity. Humans can maximize WM capacity using attention, prior to stimulus presentation (pre-cue). How attentional mechanisms operate upon WM information in higher-order cortical areas is coming into focus. To extend the current knowledge, we explore the neural correlates of attention over WM in crows. We recorded single-cell activity in two crows (*Corvus corone*) performing a change detection task. Like in chapter 1, we used a spatial pre-cue to direct attention to a spatial location in a three-stimulus array, in combination with no-cue conditions. We recorded simultaneously in the ventrolateral nidopallium caudolaterale (vLNCL), the corvid functional analogue of the prefrontal cortex, and in a new NCL area, the medial NCL (mNCL). This area, full of dopaminergic innervations in different corvids species, has lately being postulated as a new multimodal region.

We found that crows benefit from pre-cue trials and that the neural mechanisms mirror the behavioral benefits only in the vLNCL: on cued-locations, attention enhanced the neuronal information for color and location compared to un-cued location. In parallel, selective attention suppressed the color representations for those locations that were not relevant for the goal. Importantly, in the vLNCL the pre-allocation of attention retained the location information to facilitate the major color information encoding of the comparison-colors at the cued location. The effects of attention on the magnitude

and coherence of perceptual representations in the vINCL, demonstrate several similarities with effects seen in prefrontal and in higher-order areas. Contrarily, these effects were not present in the mNCL: this area was not engaged in WM processes under the visual domain.

Together, our findings elucidate the neural mechanisms by which information held in WM is modulated under attention in crows.

Keywords: cue effect, single-unit recording, crows, attentional control, working memory.

Introduction

Attention and WM (WM) are essential aspects of our cognitive capacities. The success in performing complex tasks depends critically on the ability to selectively process information from the environment (attention) and to retain information in an accessible state over time (WM) (Fougnie, 2008). Given the restricted resources of WM, it is important to allocate attention on relevant information to fulfill the goal-directed behavior (Ku, 2018). To highlight the close coupling of attention and WM, there are memory tasks, like change detection tasks, in which the participants are presented with a memory array containing visual items. After a brief delay, memory is tested with a comparison-array and participants are asked to judge whether the comparison-array changed compared to the memory array (Souza & Oberauer, 2015). Several stages of processing and neural representations occur in the absence and presence of stimuli: encoding of the items of the memory array, the maintenance in the delay period and finally, the retrieval of the relevant items from the sample-array, and comparison of the probe-array, for decision-making and responding. Each of these stages is important in determining memory performance outcome, and the benefits from selective and focused processing (Gazzaley and Nobre, 2011). Furthermore, adding a spatial or a feature-based cue before a memory array (pre-cue) can improve performance. The cue can engage attention to assist a restricted WM capacity (Broadbent, 1958; Kinchla, 1992; Treisman, 1960) and the behavioral benefits are increased accuracy, enhanced detection rates and decreased reaction times (Carrasco, 2011; Castiello & Umiltà, 1990; Fazekas & Nanay, 2017; Posner, 1980).

Our understanding of WM's neural basis began with the pioneering work of Fuster, Goldman-Rakic, and colleagues (Fuster & Alexander, 1971; Goldman-Rakic, 1995) where they found that neurons in higher-order cortex, especially the PFC, show spiking during memory delays of WM tasks (Fuster and Alexander, 1971; Goldman-Rakic, 1995; Lundqvist, Herman, & Miller, 2018). Since that, this “delay activity” is widely accepted to reflect active maintenance of the remembered stimulus in WM (Funahashi et al., 1989; Fuster & Alexander, 1971; Miller et al., 1996; Veit et al., 2014). Instead, selective attention, at the neuronal level, is thought to cause a top-down modulation of neuronal activity in sensory areas enhancing the neural signals that encode the stimulus-features (Fazekas & Nanay, 2017). Single-cell recordings from behaving monkeys have identified different forms of attentional modulation of neuronal responses in the sensory cortex, specifically in visual

areas and visual middle-temporal area (Ardid, Wang, & Compte, 2007). Attention modulates sensory neurons amplifying neural responses (Carrasco, 2011), sharpening response functions (Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006), and remapping receptive fields (Anton-Erxleben & Carrasco, 2013; Fazekas & Nanay, 2017). Moreover, attention can amplify neural responses via additive effects like increasing baseline activity (Buracas & Boynton, 2007; Carrasco, 2011; Chawla, Rees, & Friston, 1999; Cutrone, Heeger, & Carrasco, 2014; J. H. Reynolds, Pasternak, & Desimone, 2000).

Top-down modulation of sensory processing is not an intrinsic property of sensory cortices but rather include a network of multimodal regions, like the PFC and posterior parietal cortex (PPC) (Curtis & D'Esposito, 2003; Gazzaley & D'Esposito, 2007). Those area are relevant to the control of attention, including several subregions of the PPC (the lateral intraparietal area (LIP) within the intraparietal sulcus (IPS) and the superior parietal lobule) and subregions of the PFC (the frontal eye field (FEF) and the supplementary eye field), as well as the superior colliculus, for the control of voluntary eye movements (Yantis, 2008; Wang et al., 2015). For example, Zhou and Thompson (Zhou & Thompson, 2009) trained monkeys to report (with an eye movement) which of two items was brighter, after a cue indicated the position of the target. Single activity of frontal eye field neurons exhibited an increase in activity when the cue indicated that a target was about to appear in the receptive field, but not elsewhere. This increase in activity was interpreted by the authors as providing an attentional control signal to early visual areas, enhancing the perceptual representations and improving the detection (Yantis, 2008). Other studies support a similar neural modulations from PFC and parietal regions in the prioritization of information in the service of WM (McNab and Klingberg, 2008; Gazzaley, 2011; Gazzaley & Nobre, 2012; Murray, Nobre, & Stokes, 2011; Rutman, Clapp, Chadick, & Gazzaley, 2010; Zhou & Thompson, 2009). Spatial attention can activate a spatial WM signal specifying a location that should be monitored for the occurrence of a target. The delay activities of PFC neurons are spatially tuned and hence, the remembered location can be encoded as the preferred location of the most active neurons in the population (Matsushima & Tanaka, 2014). Here, the neural correlates of either process would be delay activity (Fuster, 1973). Thus, it is often difficult to examine the effects of attention and WM separately because the two processes are highly interactive (Awh & Jonides, 2001).

The behavioral and physiological mechanism that underlies WM and attentional tasks in crows, corvid songbirds, concurs comparable results. With a memory capacity that rivals monkeys (Balakhonov & Rose, 2017), crows sustain their cognitive capabilities (Emery & Clayton, 2004). For instance, crows manufacture and use tools (Weir, 2002), exhibit episodic-like memory (Emery & Clayton, 2004) and master elaborate tests of object permanence (Hoffmann et al., 2011). Lacking a laminated cortex, crows do not support their intelligence with the PFC. Instead, the anatomical substrate for WM is the nidopallium caudolaterale (NCL) (Diekamp et al., 2002; Veit et al., 2014). Many studies in birds describe NCL as an associative forebrain area representing the functional equivalent of the PFC based on electrophysiological (Diekamp et al., 2002; Kalenscher et al., 2005; Rose & Colombo, 2005), behavioral/lesion and neurochemical (Divac et al., 1985; Durstewitz et al., 1999; Metzger et al., 1996; Waldmann & Güntürkün, 1993; Wynne & Güntürkün, 1995), and anatomical studies (Kröner & Güntürkün, 1999). Corvid NCL is been already implicated in various electrophysiological studies (Nieder, 2017), supporting this notion. Neurons in NCL represent basic visual features (Wagener et al., 2018), and they can flexibly tune to different parameters, allowing for rapid change, according to task demands (Moll & Nieder, 2015; Nieder, 2017). The NCL neurons are sensitive to the encoding phase and they also temporarily maintain visual information after the stimulus disappeared (Veit et al., 2014) like delay cells in PFC.

Few studies, however, have examined the corvids' neural architecture of NCL, as the majority have focused on pigeons. Corvid NCL has been visualized in the distribution of tyrosine hydroxylase (TH) (given its high density of TH-fibers in this area) for the first time in 2013 by Nieder and Veit (Veit & Nieder, 2013). After its discovery in carrion crows (Ditz & Nieder, 2015; Veit et al., 2014), other two immunohistochemical (IHC) studies revealed the position of NCL in Eurasian jays and carrion crows (von Eugen, 2017) and house crows (Sen et al., 2019). While previous studies report NCL located as a semi-lunar area in the caudal telencephalon below the lateral ventricle (Ditz & Nieder, 2015; Veit et al., 2014), from recent IHC studies in Eurasian jay, carrion crows and house crows (*Corvus Splendens*) a different picture emerges (von Eugen, 2017; Sen et al., 2019). Here, the area of highest innervation was found to be located more medially then the previous corvid NCL, in correspondence to the shifted location of the arcopallium. From those latest studies, NCL now concerns both the medial part of NCL (mNCL) and the common ventrolateral part of NCL (vNCL), already well established in corvids literature as NCL. (Sen et al., 2019). It appears that the caudal nidopallium of the crow receives a much more widespread and varied TH-innervation compared to

the pigeon brain (von Eugén, 2017; Sen et al., 2019), which complicates delineating one specific area as the “avian PFC”. Due to its recent discovery, no electrophysiological studies in mNCL yet have confirmed its role in cognitive tasks for example testing the presence of delay activity neurons, previously found in vINCL (Veit et al., 2014).

Although many electrophysiological studies in monkeys (Colby & Goldberg, 1999; Desimone & Duncan, 1995; Itti & Koch, 2001; van Kerkoerle, Self, & Roelfsema, 2017) have revealed a number of attention-induced effects on sensory regions, considerably less work has been devoted to the higher-order brain areas employed at the source of the top-down modulatory signal of attention, like PFC and PPC. To extend the current knowledge that supports a role of those areas in gating behaviorally relevant signals, we investigate the same critical role in attention in the corvid nidopallium. We explore cognitive and neural mechanisms underlying attentional mechanisms in a visual WM task, using single-cells recordings. In light of the recent immunohistochemistry findings, we record simultaneously in the vINCL and in the mNCL to elucidate their implication in attention and WM.

We record from two carrion crows performing a change-detection paradigm, a modified version of the change detection task used in the previous chapter. In order to play the task, the birds need to remember always three colors at three different locations so that all the stages of WM processing occur in this task within pre and no-cue trials: encoding, maintenance and retrieval of the color and location (Gazzaley & Nobre, 2012). The task allows dissociating the cue effect on the information of location and color of multiple stimuli in the different stages of WM, thanks to the no-go periods of the trial under head-tracking system of unrestrained birds until the final choice.

Analyzing the activities of vINCL and mNCL neurons, separately for cue and no-cue conditions, can reveal the underlying neural mechanisms that support the attentional modulation upon relevant perceptual and WM representations in the corvids.

Materials and Methods

Subject

Two hand raised male carrion crows (*Corvus corone*), 3 years of age, with baseline weights of 505 and 500 g, were used. The crows were housed in a social group of 5 birds in an indoor aviary

with a controlled 12 hours day/night cycle. When not in experiments, the birds were given ad libitum access to water, grit and food (Versele Laga Nutribird F16, BeoSoft, occasionally nuts, fruit, chicks and mealworms). During experiments the crows were maintained on a controlled food protocol with free access to water and grit. Food-pellets (Nutribird F16, Versele-Laga, Germany) and mealworms were used as reward. The animals' body weight was controlled daily and maintained between (85 and 95 % of their baseline weight). All preparations and procedures were performed according to the principles of the care and use of laboratory-animals adopted by the German Animal Welfare Law for the prevention of cruelty to animals and were conducted after approval by the LANUV (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen).

Experimental setup

The setup consisted of a chamber (50 cm (width) x 50.5 cm (depth) x 77.5 cm (height), equipped with a remote monitoring camera (Sygonix, Taiwan), a 22" touchscreen-monitor (ELO 2200L APR, Elo Touch Solutions, Inc), and a custom-made automatic pellet feeder (plans available: www.jonasrose.net). The bird was placed on a wooden perch in front of the touchscreen such that the maximum distance from the bird's eye to the screen was 7 cm. The animal's head position and rotation were tracked in the horizontal and vertical plane, using two computer-vision cameras (Chameleon3, Point Grey Research Inc., Richmond, BC, Canada). For tracking, a custom 3D-printed reflector was mounted on a lightweight surgically implanted head-post and removed after each experimental session. The frame rate of the cameras were 75 Hz and data were smoothed by integrating over 2 frames using custom code on a control PC. All experiments were controlled by custom programs in Matlab (Mathworks inc. Natick, MA USA) using the Biopsychology (J. Rose, T. Otto, L. Dittrich, 2008) and Psychophysics toolboxes (Brainard, 1997). Digital input and output of the control PC was handled by a microcontroller (ODROID C1, Hardkernel co. Ltd) running custom software (available: www.jonasrose.net) connected through gigabit network. This allowed for flexible and temporally precise IO-communication.

Behavioral protocol

The crows were trained on a change detection task (Fig. 6), a modified version task used in the previous chapter (chapter 1). Each bird was tested daily. During experimental sessions, periodically brief breaks with access to water was offered to the animals.

Each trial began with an inter-trial interval (4000 ms). Following the inter-trial interval, animals was first presented a red fixation dot in the center of the screen (maximal 5000 ms). Two camera-based head-tracking units allowed the crows to visualize the stimuli only with their left eyes. The crows had to hold their head still (less than ± 2 cm horizontal or vertical displacement) and look straight at the center of the screen (less than $\pm 17^\circ$ horizontal or vertical rotation) to initialize and complete the trial. Moving their head before the final response period, resulted in an aborted trial. Each training session consisted of a randomized order of two conditions: a no-cue condition and a pre-cue condition where the cue is prior to sample presentation. In the no-cue condition, after a short delay of 600 ms, an array of 3 colored squares appeared for 400 ms on the left side of the screen and had to be maintained in WM for 1000 ms. In the pre-cue condition, we used a spatial cue, a white circle appears for 200 ms to direct attention to a spatial location of where the change might occur. Following the pre-cue there was a brief delay of 400 ms. Importantly, both the no-cue and pre-cue conditions had the same retention interval.

At the end of each condition, during the comparison period the sample-array re-appeared for 400 ms, either identical to that shown before the cue period, or with one of the three colored squares changed. After 400 ms, the colored squares turn gray in the choice period, and a square appeared in the center of the screen. Crows were rewarded for indicating if there was no change, by pressing the new centered square available, or if there was a change, by pressing any of the peripheral squares within 4000 ms. As reward, one single pellet (Nutribird F16) was delivered to a holder on the automated feeder which was illuminated during reward-delivery for 2000 ms. An incorrect response, or failure to respond, was mildly punished by briefly flashing the screen white and with a time-out (9000 ms).

The stimuli were based on the protocol by Buschman et al. (2011). Each day three random color-combinations were chosen from a set of 14 color combinations such that three pairs (color 1 and color 2), one for each stimulus-location were chosen on a given day. Thus, on each training day, one random pair of colors was fixed to each of the three stimulus locations. The order of presentation of the colors within a pair was randomized and balanced across trials. Color-stimuli were square, 10

degrees of visual angle (DVA) on the left side of the screen and placed either on the horizontal meridian of the screen or 45.8 DVA above/ below the meridian at a distance from the center of 54 and 55.4 DVA (center of the stimulus) respectively (Balakhonov & Rose, 2017). The cue stimuli were white thin transparent circles of 11 DVA, positioned on the exact location of the color-stimuli to cue. The maximal binocular overlap for carrion crows is around 37.6 DVA (Troscianko et al., 2012); thus, all color-stimuli and cues were placed well outside the binocular area, taking into account head-movement, head-rotation and eye movement.

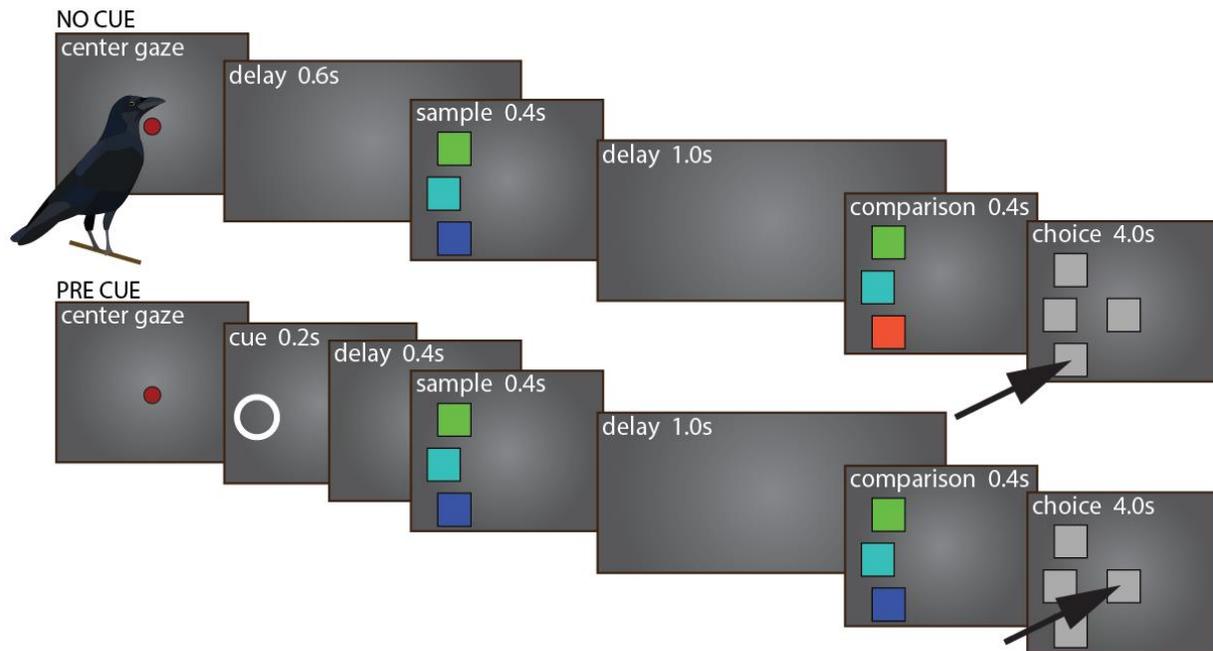


Figure 6. Behavioral protocol: the change detection task (pre-cue).

The crows were trained on a change detection task. The crows had to hold their head straight at the center of the screen to initialize and complete the trial. Following the inter-trial interval (4 s), animals were presented a red fixation dot in the center of the screen (maximal 5 s) to ensure the head position. Each training session had a randomized order of a no-cue and a pre-cue condition. In the no-cue condition, after a delay of 0.6 s, an array of 3 colored squares appeared for 0.4 s on the left side of the screen (sample). In the pre-cue condition, we used a white circle (0.2 s) prior sample-onset, over a location of where the change might occur. Following the pre-cue there was a brief delay of 0.4 s. After a delay of 1 s in both conditions the sample-array re-appeared either identical or with one of the three colored squares changed in the comparison-array. After 0.4 s, the colored squares turn gray during the choice period, and a square appeared in the center of the screen. Crows were rewarded for indicating no change (pressing the centered square) or a change (pressing any of the peripheral squares) within 4 s.

Surgery

All surgeries were performed under aseptic procedures. Before surgery, animals were induced by ketamine (50mg / kg) and xylazine (5 mg / kg). Once deeply anaesthetized, animals were placed in a stereotaxic frame with the anterior fixation point (i.e., beak bar position) 45° below the horizontal axis of the instrument (Karten & Hodos, 1967). For the head tracking system, a light-weight head-post was chronically implanted to position a small silver colored reflector during behavioral experiments. Few feathers were plucked over the base of the beak exposing skin for a small incision to retract the skin. A small opening was drilled in the surface of the bone in order to expose the *trabeculae* to which the head-post was attached with dental acrylic. The wound-margins were sutured. For the electrodes' implantation, we chronically implanted two microdrives with two 32-channel microelectrodes each, and two connectors for the head stages on the right hemisphere, using stereotaxic coordinates (center of craniotomy for NCL: anteroposterior (AP) 5 mm; mediolateral 13 mm; center of craniotomy for NID: AP 5 mm; mediolateral 6 mm). Following the administration of analgesia (morphasol, 3 ml / kg) the animal was placed in a recovery-cage until fully recovered. At the time of thesis submission, both crows were still used in ongoing experiments, therefore no histological or electrode-MRI data are available for the current study.

Neurophysiological recordings

Recordings were performed using two chronically implanted 32-channel microelectrodes (Neuronexus Technologies Inc., Ann Arbor MI) in the right hemisphere. The distance between recording sites was 50 μm (active zone of 1550 μm). Both implanted regions were recorded simultaneously. Microelectrodes were mounted on movable microdrives (Neuronexus Technologies Inc., DDrive). The signal was amplified, filtered and digitized using Intan RHD2000 headstages and USB-Interface board (Intan Technologies LLC, Los Angeles CA). The system also recorded digital event-codes that were sent from the behavioral control PC using a custom IO-device (www.jonasrose.net).

Prior to each recording session the electrodes were advanced (750 μm) using the microdrives. Recordings were started 20 minutes after the advancement. The signals were recorded at a sampling rate of 30 kHz and filtered with a bandpass filter (0.01 Hz – 7.5 kHz). The recorded neuronal signals were not pre-selected for task involvement.

The sorting of the recorded waveforms was performed using the semi-automatic klusta-suite software (Rossant et al., 2016), making use of the high electrode count and their close spacing, in order to isolate signals originating from single cells, and to separate signals with similar wave forms from each other. Using this software, the spatial distribution of the signal along the different electrodes was taken into account in order to untangle overlapping signals.

Data analysis

Data was collected and analysed with Matlab (Mathworks inc. Natick, MA) using custom code and commercial toolboxes (Curve Fitting Toolbox Version 3.5.3, Statistics and Machine Learning Toolbox Version 10.2). For all statistical tests, a significance level of $\alpha = 0.05$ was assumed. The behavioral data analyses were based on attempted trials, therefore excluding gaze-breaks trials which were analysed independently. All the behavioral measures, the effects of no-cue and pre-cue and number of stimuli on performance, gaze-breaks, reaction time, sensitivity score for change/no-change discrimination (d' score) (Green & Swets, 1966), and memory-capacity measurement (Pashler k ; Rouder et al., 2011) were tested with t-test with cue-type as independent variables across days. T-tests were conducted for each crow independently. A one-way analysis of variance (ANOVA) was applied to test location preferences.

The neural data analyses were based on correct trials to ensure that crows were fully engaged. Each neuron was tested by means of ANOVA, followed by Tukey-Kramer Honest Significantly Different (HSD) post-hoc analysis. To quantify the factors affecting the firing rates of all neurons, we calculated the percent explained variance (PEV). The main parameter (ω^2) is a measure for the percentage to which the variation of data is explained by the tested factor. Calculated from the sum of squares of the effect (SS_{effect}) and the mean squares of the within group (error) variance (MS_{error}). The single-neuron activity and the population PEV-analysis during the task was analysed with a bin size of 200 ms and a step size of 50 ms.

$$\omega^2 = \frac{SS_{effect} - df * MS_{error}}{SS_{total} + MS_{error}}$$

A permutation test was used to test if the calculated effect sizes were significantly different from chance. For this test the dataset was permuted randomly 1000 times and the corresponding random-PEV calculated each time. By ranking the real PEV-value in relation to the random-PEV the likelihood of finding the PEV-value by chance is estimated from the actual distribution of the data. Therefore, it does not make any assumptions about the distribution of firing rates (Bower, 2012) across different experimental conditions, and returns an unbiased estimate of the likelihood of generating a particular effect size within the data randomly (Buschman et al., 2011).

To quantify the effect of the cue on the color information carried at each of the three locations, we calculated the PEV which measured for each cell the proportion of variance in firing rate that could be explained by color identity (color 1 vs. color 2, from the sample or from the comparison-array) (Lundqvist et al., 2016). The PEV by the factor color was calculated independently at each location for all the possible task conditions: pre-cue presented at the considered location, no-cue at the consider location and pre-cue presented at another location (irrelevant location). We calculated the PEV specifically for each different task-period: sample, delay after the sample offset (here divided in early delay and late delay) and comparison period. The PEV by the factor change - no-change was used to quantify the effect of the cue on the change detection. Furthermore, the PEV by the factor cue-presence (pre-cue at each location vs. no-cue in the whole sample-array) was included to estimate the effect on the entire population of each area of the cue presence. To this, we added an analysis of the PEV by the factor location, thus comparing the effect of pre-cueing on each location and separately also the no-cue effect on each location.

Results

Behavioral results

Two naïve hand raised crows (*Corvus corone*) were trained previously on a change detection task for approximately 4 months, after which we performed electrophysiological recordings for 34 days for crow FRN and for 12 days for crow JRO. Here, we report the behavioral and electrophysiological results of those days.

FRN and JRO performed 850 trials daily. Both birds showed a higher percent correct in the pre-cue conditions compared to the no-cue condition (Fig. 7A; t-test FRN: $t(33) = -28.30$, $p < .001$ JRO: $t(11) = -9.63$, $p < .001$).

We used the sensitivity score for change/no-change discrimination (d' score)(Green & Swets, 1966). The d' score was calculated using the following equation:

$$d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$$

Hit rate was defined as the conditional probability that the birds responded “change-present” given that the change was presented, and the false-alarm rate was defined as the conditional probability that the birds responded “change-present” when the change was absent. In both birds, the change detection accuracy d' increased in the pre-cue condition (Fig.7C; t-test FRN: $t(9) = -8.86$, $p < .001$ JRO: $t(9) = -2.51$, $p = .02$).

WM-capacity measurement (Pashler K, Rouder et al., 2011) was calculated using the following equation:

$$\hat{k}_p = N \left(\frac{\hat{h} - \hat{f}}{1 - \hat{f}} \right)$$

Crows showed a higher WM capacity K on the pre-cue conditions, demonstrating an increase in information about the sample-array (Fig.7B; t-test FRN: $t(33) = -25.84$, $p < .001$, JRO: $t(11) = -9.95$, $p < .001$).

To analyze the reaction time, we calculated the time from the comparison-period to the peck response. The reaction time of correct responses is similar between the no-cue and pre-cue conditions (Fig. 7D; t-test FRN: $t(33) = -0.73$, $p = 0.46$ JRO: $t(11) = -1.36$, $p = 0.19$). Incorrect responses were significantly quicker compared to the correct responses (FRN: corr: 0.31 ± 0.01 s; incorr: $.73 \pm 0.03$ s; JRO corr: 0.34 ± 0.02 s; incorr: 0.47 ± 0.03 s; t-test FRN: $t(33) = -13.93$, $p < .001$ JRO: $t(11) = -8.21$, $p < .001$).

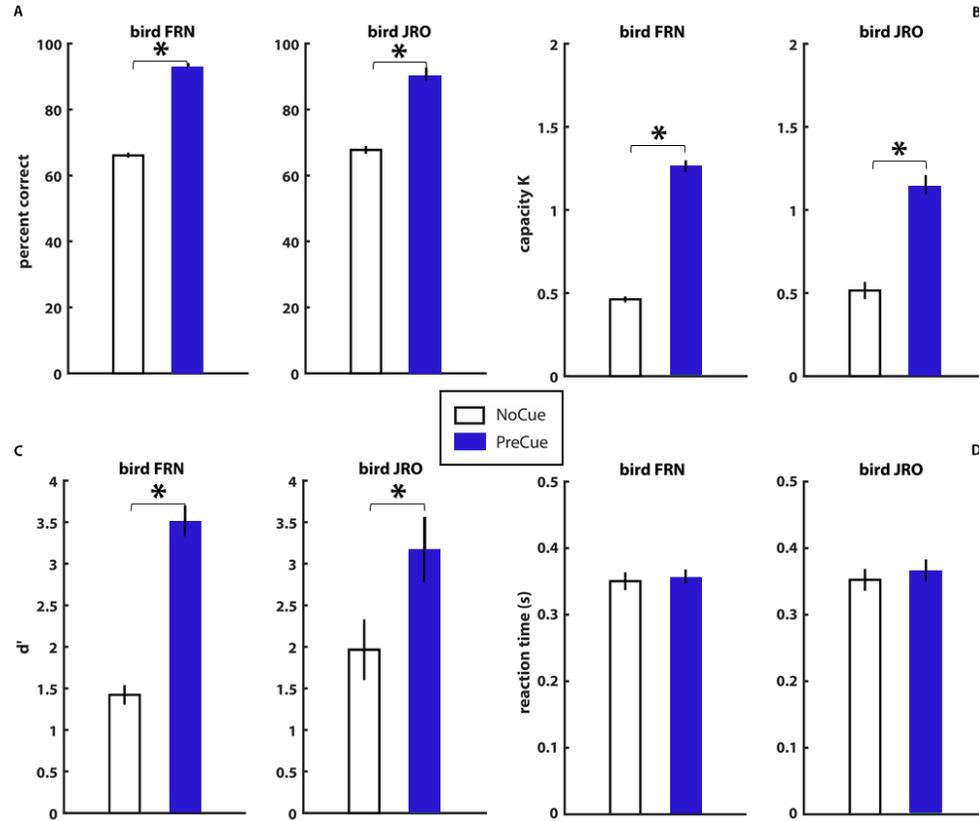


Figure 7. The cue effect.

A) Behavioral performance (percent correct) of both crows as a function of task no- and pre-cue conditions (chance level= 50 %); FRN: no-cue: 66.07 ± 0.54 %; pre-cue: 92.95 ± 0.80 %; JRO no-cue: 67.74 ± 1.11 %; pre-cue: 90.15 ± 2.25 %. B) WM capacity K as a function of no- and pre-cue conditions; FRN: no-cue: 0.47 ± 0.01 ; pre-cue: 1.30 ± 0.03 ; JRO no-cue: mean \pm SEM= 0.52 ± 0.05 ; pre-cue: 1.17 ± 0.05 . C) The sensitivity d' as a function of no- and pre-cue condition; FRN: no-cue: 1.42 ± 0.10 ; pre-cue: 3.49 ± 0.19 ; JRO no-cue: 1.96 ± 0.35 ; pre-cue: 3.16 ± 0.38 . D) Reaction time of both crows on correct trials as a function of task conditions; FRN: no-cue: 0.35 ± 0.02 s; pre-cue: 0.36 ± 0.02 s; JRO no-cue: 0.34 ± 0.03 s; pre-cue: 0.36 ± 0.03 s. Error-bars are SEM.

To determine whether there were any spatial response biases, we analysed the percent correct by location. Both crows performed a comparable high percent correct on all the three locations. ANOVA shows no significant difference between locations (Fig. 8C; ANOVA FRN: $F(2,99) = 0.89$, $p = .41$; JRO: $F(2,33) = 2.76$, $p = .07$).

A head-tracking system controlled the gaze-direction of the crows, to ensure the fixation position during stimulus presentation. Tracking allowed for control over which eye viewed the stimuli, considering their relative small binocular visual field and to prevent any strategies overcoming the location to choose (e.g. moving their head on the stimulus location to remember). Overall, there

were significantly less gaze-breaks during no-cue trials compared to cue trials (Fig. 8B; FRN: $t(33) = -31.10$, $p < .001$ JRO: $t(11) = -17.94$, $p < .001$).

The omission rate (the lack of response in the choice) was very low, only 0.31 % of the total responses for FRN and 0.13 % for JRO (Fig. 8A); FRN had a significantly higher omission rate in no-cue condition compared to the cue-condition, however there was no difference for JRO (t-test FRN: $t(33) = 3.25$, $p < .001$ JRO: $t(11) = 1.46$, $p = .17$).

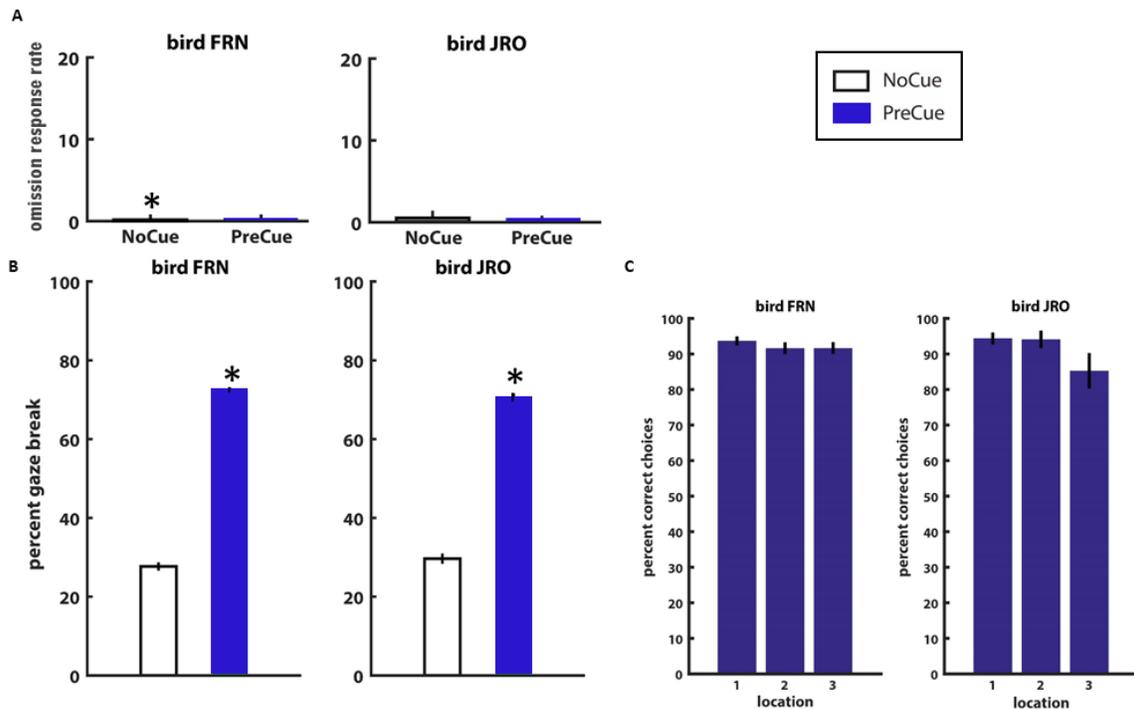


Figure 8. Behavioral bias.

A) Percent of omission rate (the lack of response in the choice) as a function of task conditions; FRN: no-cue: 0.42 ± 0.11 %; pre-cue: 0.04 ± 0.02 %; JRO no-cue: 0.18 ± 0.14 %; pre-cue: 0.08 ± 0.08 %. B) Percent of gaze-breaks of both crows on started trials as a function of task conditions; FRN: no-cue: 27.66 ± 0.71 %; pre-cue: 72.33 ± 0.71 %; JRO no-cue: 29.66 ± 1.13 %; pre-cue: 70.34 ± 1.13 %. C) The percent correct as a function of stimuli locations; FRN: loc1: 93.70 ± 1.05 %; loc2: 91.63 ± 1.28 %; loc3: 91.67 ± 1.40 %; JRO loc1: 94.39 ± 1.56 %; loc2: 94.10 ± 2.39 %; loc3: 85.27 ± 4.57 %. Error-bars are SEM.

Electrophysiological results

Cell incidence

We recorded single-cell activity of 403 neurons in vNCL (197 cells in FRN and 204 in JRO) and 121 neurons in mNCL (71 in FRN and 50 in JRO). All neurons had at least an average firing rates of 0.35 Hz and less than 1 % of consecutive spikes that violate refractory period of 1 ms. No additional criteria were used to select neurons. The analysis of neuronal activity was based on correct trials since the high performance of our birds in pre-cue trials resulted in low number of error-trials. In both birds, the majority of neurons in vNCL varied the firing rates according to the cue presence and to the sensory properties of the stimuli (color and location) (Fig. 9).

It appears the cells in vNCL are coding the location and color information during the different task periods. The example vNCL cell in Fig. 9A and C is a neuron with a significant PEV by color identity of the location 3 from the sample-array during the sample period. The cell increases the firing rate after the cue onset showing pre-sample activity (from the pre-cue onset to the related delay offset). In the pre-cue condition, the neuron at the sample period show a higher firing rate compared to the no-cue condition. The neuronal discharges after the sample onset continue in both condition throughout the early phase of the delay period and decrease in the late delay. The example neuron in Fig. 9B and D has a significant PEV by color identity from the sample-array during the delay period in the location 3; this neuron shows delay activity by increasing over each delay period. In the pre-cue condition, the neuron show a more sustain firing rate throughout the delay after the sample offset compared to the no-cue condition. Both neurons (Fig. 10) show a suppression of activity right after the comparison offset.

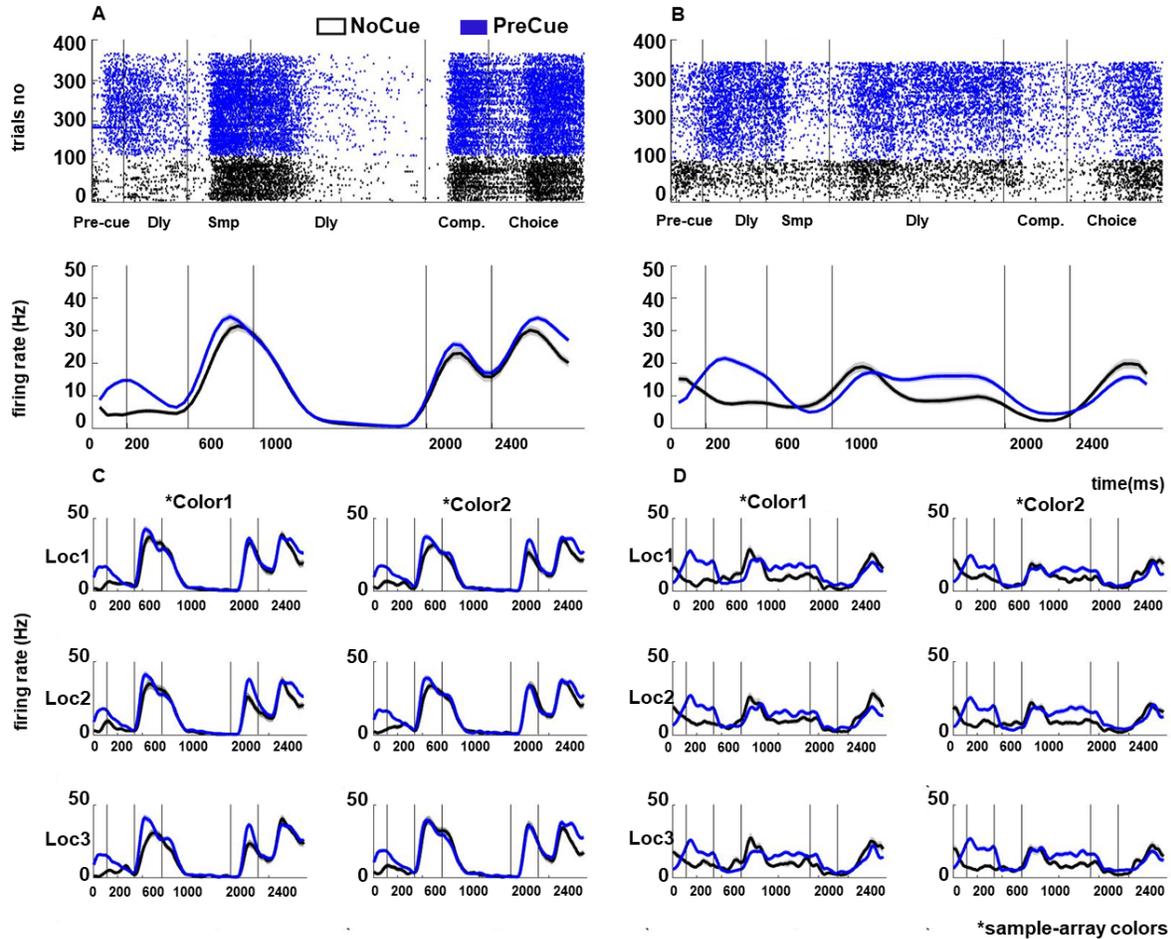


Figure 9. Example vINCL neurons.

The upper part shows dot-raster histograms (each dot represents an action potential) for the pre- and no-cue conditions of two neurons that have a significant PEV for color at location 3 during A) the sample and B) the delay periods. In the lower panels, there are averaged spike density histograms for the same cells, smoothed with a 200 ms-bins. Vertical lines mark each task periods, from the start (at 0) to the choice (at 2400 ms). C) and D) represent the averaged spike density histograms of the above cells in the conditions in which color 1 or color 2 where in the location 1, 2 or 3 in the sample-array.

To determine whether the color identity significantly affected the firing rates on the three different locations ($p < .05$), we used a nonparametric statistical approach based on permutation tests. We classified neurons with a significant different PEV by color identity (color 1 vs color 2) in at least one location as significant neurons. We ran independent analyses for the sample, delay (early delay and late delay), and comparison period based on the colors present in the sample-array. In the comparison period, we also quantify the proportion of significant neurons by the colors presented in the comparison-array. Firing rates were analysed in a 400 ms time window, except for the comparison, in which we used a 300 ms time window. We removed 100 ms during the first phase

of firing activity in the sample and comparison period to account for the sensory latency of the visual response, and 200 ms in the delay period to exclude potential sensory offset activity (Moll & Nieder, 2016).

In vNCL (Fig. 10A), different neurons showed a significant PEV by color (from the sample-array colors) during the sample ($n = 189$, 46.9 %), the early delay ($n = 140$, 34.7 %) and the comparison period ($n = 87$, 21.6 %). In mNCL (Fig. 10B), significant neurons were also present during the sample ($n = 18$, 14.8 %), delay ($n = 23$, 19.0 %) and comparison ($n = 19$, 15.7 %). We also calculated the proportion of significant neurons for the colors presented in the comparison-array in vNCL ($n = 160$, 39.7 %) and mNCL ($n = 27$, 22.3 %) during the comparison. Both NCL regions had a significantly different proportion of significant cells in the three locations (vNCL: $F(2,21) = 5.02$, $p = .01$; mNCL: $F(2,21) = 3.85$, $p = .03$), with a higher proportion for location 1 (vNCL: $M = 33.37$, $SD = 4.05$; mNCL: $M = 5.12$, $SD = 0.61$) compared to location 2 and location 3. In both regions there was an overlap of significant neurons based on the sample-array colors from sample to early delay (vNCL $n = 84$, 44.4 %; mNCL $n = 4$, 22.2 %), sample to comparison (vNCL $n = 20$, 10.6 %; mNCL $n = 21$, 38.8 %) and from early delay to comparison (vNCL $n = 19$, 13.5 %; mNCL $n = 7$, 91.3 %). The late delay had a contribution of 5.0 % in vNCL and 10.0 % in mNCL.

Next, we analysed what fraction of neurons showed a visual response independent of the task-context (Fig. 10). This would be the case if a neuron was responsive to the sample-array in the sample period and to the comparison-array in the comparison period. The fraction of neurons with a mutual visual response was from the sample period (sample-array) to the comparison period (comparison-array) (vNCL $n = 51$, 27.0 %; mNCL $n = 6$, 33.3 %). We analysed what fraction of neurons showed a delay activity and a visual response independent of the task-context, like if a neuron was responsive to the sample-array in the delay period and to the comparison-array in the comparison period. Thus, we compared the overlap from early delay (sample-array) to the comparison (comparison-array) (vNCL $n = 24$, 17.1 %; mNCL $n = 22$, 95.6 %). The overlap was also from the comparison period recalling the sample-array colors to the comparison period of the new encoded comparison-array colors (vNCL $n = 39$, 44.8 %; mNCL $n = 6$, 31.6 %).

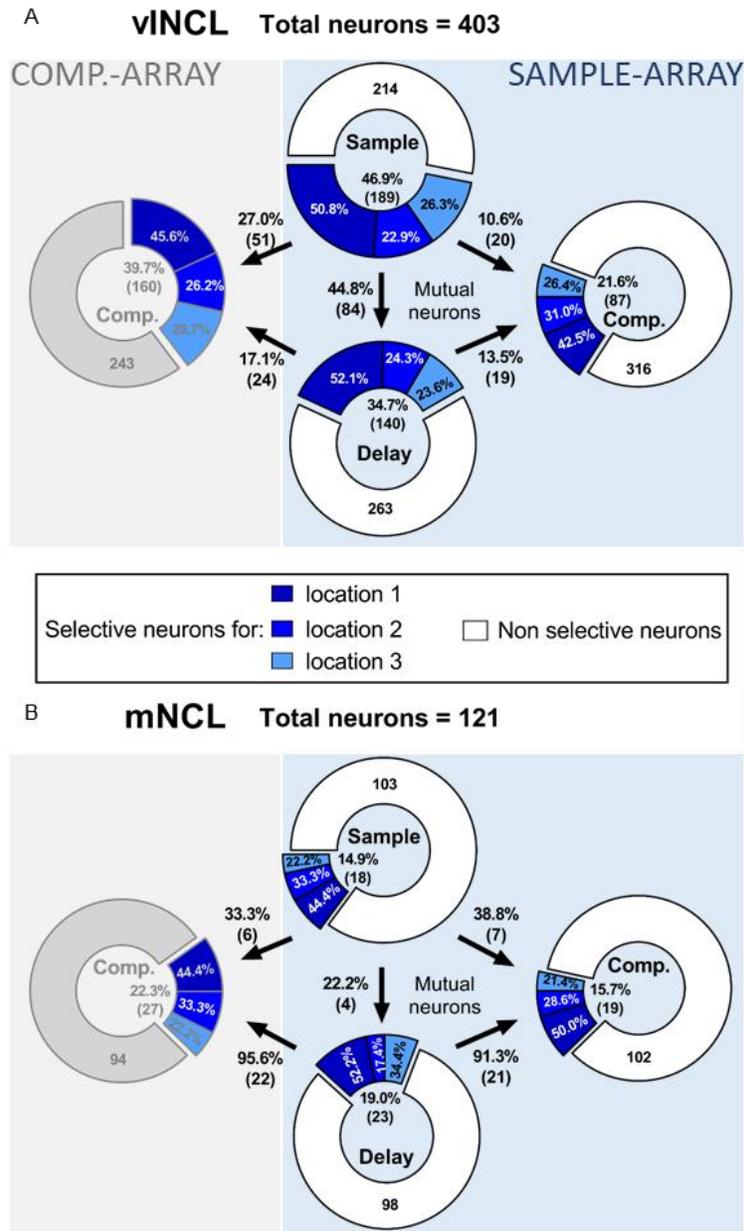


Figure 10. Significant neurons.

Percent of neurons that show a significant PEV by color identity (color 1 vs color 2) at each of the three locations. A) In the vINCL significant neurons based on the sample-array colors (light blue background) during the sample, delay and comparison period. The proportion of significant neurons for the colors presented in the comparison-array during the comparison period are on the left (gray background). B) The significant neurons in mNCL during the different task periods. In both regions there was an overlap of significant neurons between the different task periods (the arrows indicates the directions of the mutual selectivity between the period from the sample-array colors).

In contrast to the vNCL, significant neurons in mNCL during the sample (Fig. 11A) and the delay (Fig.11B) exhibited no net modulation during the entire task period, without any clear difference between the pre-cue and no-cue condition. The absence of firing rates modulation contest specific of the task is consistent with the peculiarity of this area of a high overlap of mutual significant cells between the task period analysed (Fig. 10B).

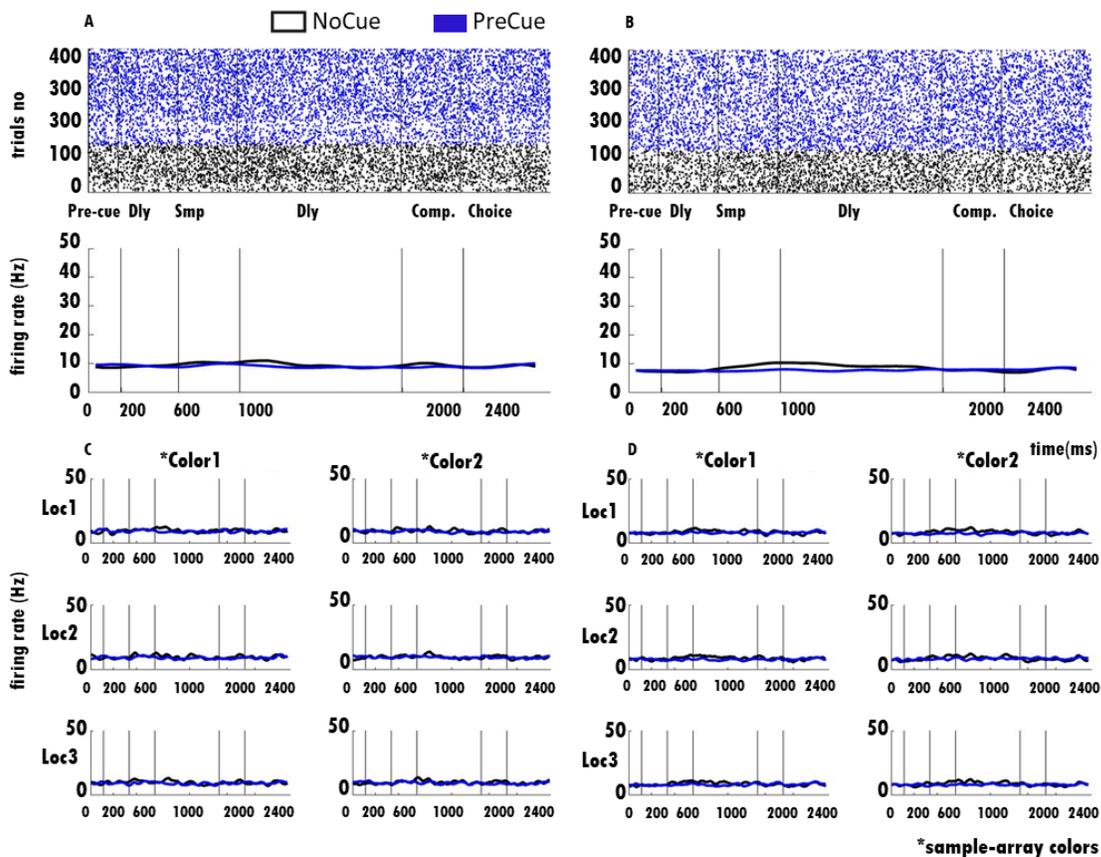


Figure 11. Example mNCL neurons.

The upper part shows dot-raster histograms (each dot represents an action potential) for the two conditions (pre- and no-cue) of two neurons that show a significant PEV for color in location 1 during A) the sample and B) the delay periods. In the lower panels there are averaged spike density histograms for the same cells, smoothed with a 200 ms-bins. Vertical lines mark each task periods, from the start (at 0) to the choice (at 2400 ms). C) and D) represent the averaged spike density histograms of the above cells in the conditions in which color 1 or color 2 where in the location 1, 2 or 3 in the sample-array.

Population analyses

We applied population analyses based on the entire population of recorded neurons for each region to evaluate the neuronal activity selected at different task periods. All neurons in vINCL ($n = 406$) and in mNCL ($n = 121$) were examined using a one-way ANOVA with factor color identity (color 1 vs color 2 from the sample- and comparison-array) at the three locations independently for each cue-condition. One-way ANOVA was run separately for each task period (sample, delay (early delay) and comparison (with colors from the sample- and comparison-array) period).

To quantify the color information carried at each of the three locations, we calculated the PEV, which measured for each cell, the proportion of variance in firing rate that could be explained by color identity (color 1 vs color 2) (Lundqvist et al., 2016). The strength of the color identity at each of the three locations is in percentage. For each neuron, the location with the highest PEV effect by color identity was included to represent the “preferred” location carrying the strongest difference between color 1 vs color 2 and thus, the highest color representation in the population analysis. Each neuron at its preferred location was used to calculate the PEV (bin size of 200 ms and step size of 50 ms) by color identity in the entire trial period for each of the three possible conditions of the task: at each location the color information was compared against the presence of a pre-cue, in the absence of cues or in the presence of pre-cues at another location (irrelevant location).

In order to determine if the cue had an effect on color-processing, a one-way ANOVA, with color identity as the factor, was used on the PEV for color at the “preferred” location. We compared pre-cue, no-cue and irrelevant locations to see if there was a difference in overall activity for color identity from the population. The ANOVA showed that the effect of PEV for color was significantly different for all the considered task periods in vINCL (Fig. 12A, C, E, G; Sample: $F(2,1172) = 27.91$; $p < .001$; Delay: $F(2,1161) = 20.41$; $p < .001$; Comparison, sample-array: $F(2,1171) = 5.14$; $p = .005$; Comparison, comparison-array: $F(2,1172) = 20.87$; $p < .001$). Post-hoc analyses using the Tukey-Kramer HSD indicated that in the sample, in the early delay and in the comparison (only from the comparison-array colors) the vINCL population had a significantly higher PEV at the cue-condition (Sample: $M = 0.017$, $SD = 0.00$; Delay: $M = 0.009$, $SD = 0.00$; Comparison, comparison-array: $M = 0.015$, $SD = 0.001$) compared to the no-cue (Sample: $M = 0.012$, $SD = 0.000$; Delay: $M = 0.005$, $SD = 0.000$; Comparison, comparison-array: $M = 0.009$, $SD = 0.001$), thus demonstrating a higher color coding for cued locations when compared with no-cue location trials.

Moreover, in order to compare the color coding of attentive stimuli to the irrelevant stimuli for the task goal, we compared the PEV by color in pre and no-cue against the irrelevant location. In all task periods, including the comparison period, the pre-cue (Comparison, sample-array: $M = 0.04$, $SD = 0.00$) and no-cue (Comparison, sample-array: $M = 0.004$, $SD = 0.00$) location were significant different when compared to the irrelevant location, the location in which the pre-cue was in the not consider location (Sample: $M = 0.001$, $SD = 0.00$; Delay: $M = 0.001$, $SD = 0.00$; Comparison, sample-array: $M = 0.001$, $SD = 0.00$; Comparison, comparison-array: $M = 0.04$, $SD = 0.00$). We plotted the PEV by color to visualize the temporal evolution of the overall population in the entire task period (Fig. 12A, C, E, G) and restricted to only significant neurons (Fig. 12B, D, F, H).

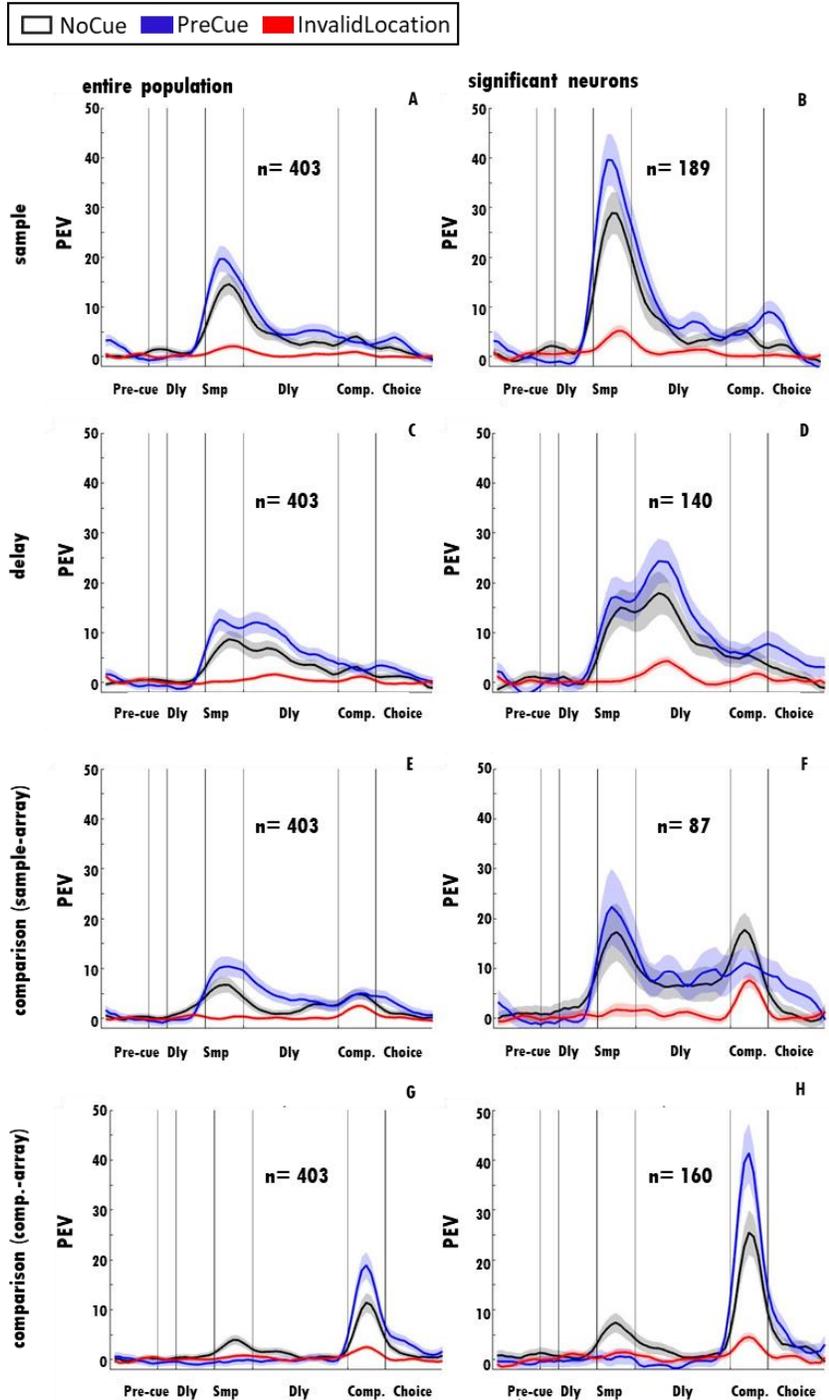


Figure 12. PEV by color in vINCL.

In order to determine if the cue had an effect on color-processing, we calculated the PEV for each neurons of the population during A) the sample, C) the delay, E) the comparison (for the sample-array), G) the comparison (for the comparison-array) at the preferred locations for no-cue (black), pre-cue (blue) and invalid locations (red) for different task-periods. The PEV by color constricted to only significant neurons for the sample-array during B) the sample, D) the delay, and F) the comparison and for the comparison-array in H) the comparison. The shaded areas are SEM.

In addition, to quantify the effect of the cue presence in the trial, we calculated the PEV by the factor “cue presence” using pre-cue at each of the three locations and the no-cue condition as whole-array (Fig. 13A). We also calculated the PEV by the location information detected by pre-cue and no-cue specified at each of the three locations (Fig.13B). From the start to the comparison period, the vINCL showed a high degree of differentiation for the cue presence and a high discrimination of the three locations in pre-cue only.

Furthermore, we analysed the PEV effect on the entire population by change/no change separately at the no-cue and the pre-cue condition. In the vINCL, we found a very clear change/no change effect on the comparison period that does not depend on the pre or no-cue condition (Fig. 13C; vINCL: t-test: $t(387) = 1.03, p = .30$).

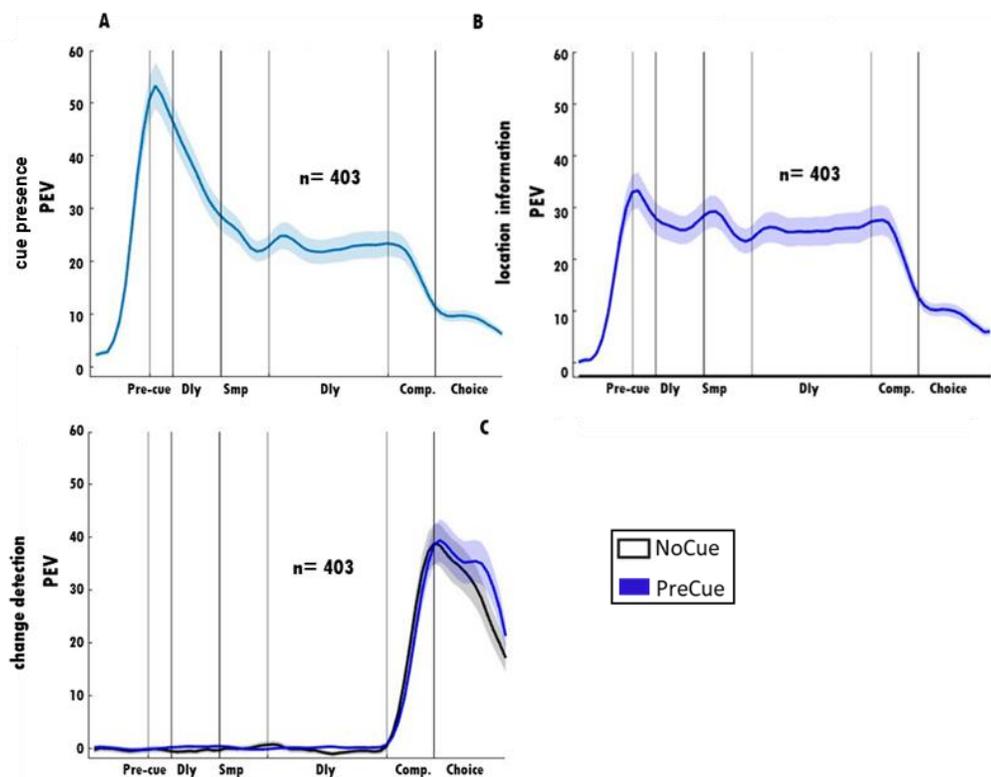


Figure 13. PEV by location and by change detection in vINCL.

A) PEV by the cue presence, detected by pre-cue at each of the three locations and the no-cue as whole-array in the entire population B). PEV by the location information detected by pre-cue and no-cue in the entire population. C) PEV by change detection separately at the no-cue and at the pre-cue condition in the entire population. The shaded areas are SEM.

In mNCL, we also compared pre-cue, no-cue and irrelevant locations to determine whether there was a difference in overall activity for color identity from the population (Fig. 14A-E). The PEV of the cue-condition was not different during the task (Sample: $F(2,348) = 3.28$; $p = 0.13$; Delay: $F(2, 348) = 0.89$; $p = .40$; Comparison, sample-array: $F(2, 351) = 0.48$; $p = .61$; Comparison, comparison-array: $F(2, 348) = 0.28$; $p = .75$).

The PEV of the entire population of the mNCL by the factor cue presence (Fig. 14E) and by the location information by pre- and no-cues (Fig. 14F) does not convey significant information of the task parameters analyzed.

The PEV effect on the entire population by change/no change separately at the no-cue and the pre-cue condition (Fig. 14G) does not depend on the pre or no-cue condition, with a smaller effect compared to the vNCL (vNCL: t-test: mNCL: $t(116) = -1.46$, $p = .14$).

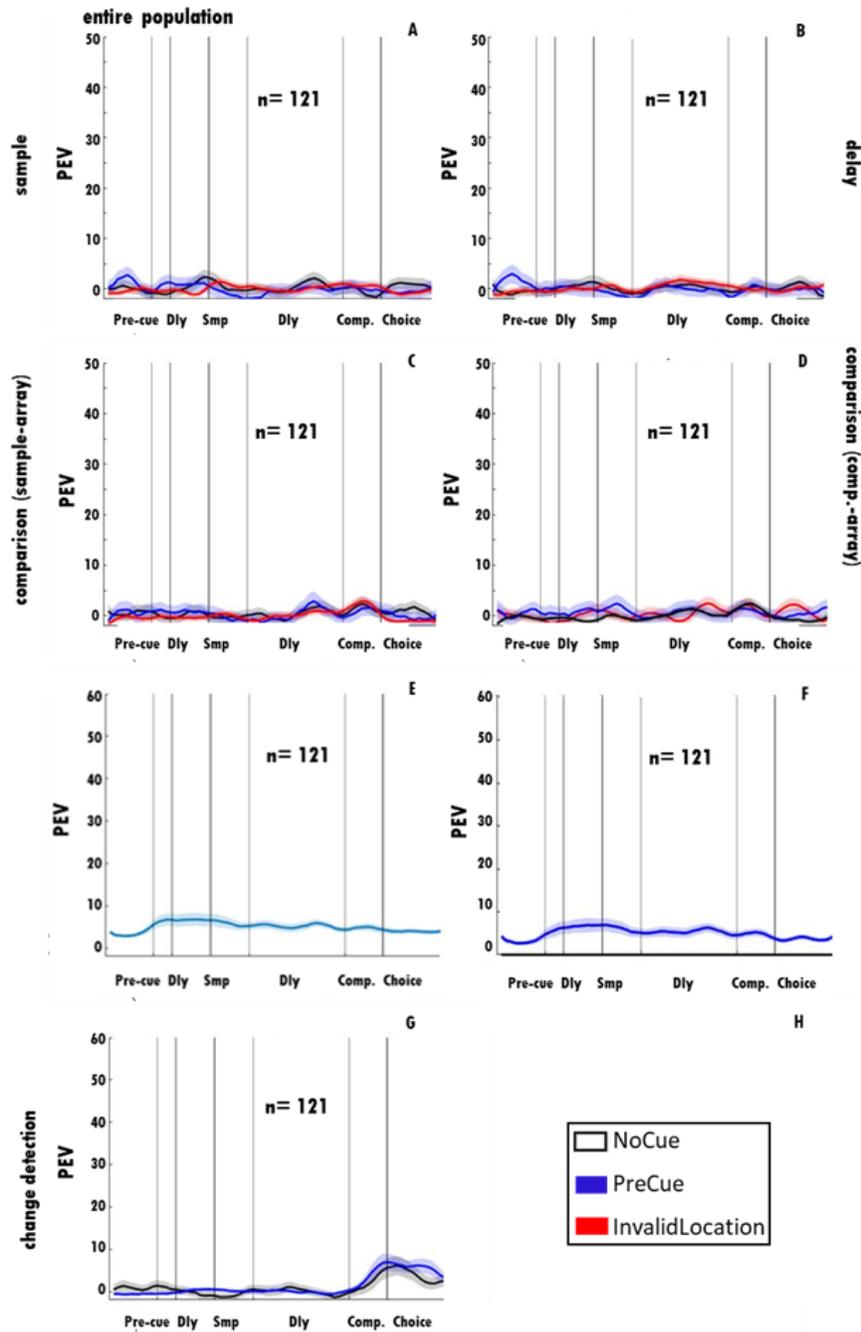


Figure 14. PEV analysis in mNCL.

In order to determine if the cue had an effect on color-processing, we calculated the PEV for each neurons of the population during A) the sample, B) the delay, C) the comparison (for the sample-array), D) the comparison (for the comparison-array) at the preferred locations for no-cue (black), pre-cue (blue) and invalid locations (red) for different task-periods. E) PEV by the cue presence, detected by pre-cue at each of the three locations and the no-cue as whole-array in the entire population. F) PEV by the location information detected by pre-cue and no-cue in the entire population. G) PEV by change detection separately at the no-cue and at the pre-cue condition in the entire population. The shaded areas are SEM.

Discussion

Consistent with my previous chapter, here crows confirm their ability to utilize attentional cues to optimize their performance in a change-detection task. Crows benefit behaviorally from pre-cue trials increasing the percent correct, the change detection accuracy and increasing dramatically the capacity K . The pre-cue effect can now be analysed not only at behavioral level, but also at neuronal level through single-cell recordings. The birds needed to remember three colors at three different locations such that all the stages of WM processing (encoding, maintenance and retrieval) occur within pre and no-cue trials to allow a neuronal investigation (Gazzaley & Nobre, 2012). The protocol profits from a head-tracking system of unrestrained birds in the different no-go periods until the final choice. The no-go periods are useful to prevent possible motor artifacts.

In this study, we recorded 403 neurons from vINCL and 121 neurons in mNCL. Many neurons modulated significantly their firing rates by different task factors (colors, locations or cue presence) in different time period of the task. To access the effect of pre-cue on WM contents for the factor color, we based our analysis on the entire population, selecting the maximal color information carried by each neuron between the three locations and for each task period (sample, delay and choice). Task modulated neurons are presented mainly in the vINCL, the avian multimodal association area already reported in different electrophysiological studies (Ditz & Nieder, 2015, 2016; Moll & Nieder, 2015; Veit et al., 2014; Veit & Nieder, 2013), but also also in the mNCL, the latest discovered area with a high density in basket cells. However, our findings differed between the two regions.

The vINCL

Color information processing

Consistent with the behavioral benefits in WM, the focus of attention in corvids vINCL have revealed attentional mechanisms that operate throughout neuronal excitability at different stages of the color information processing.

Sample period analysis: stimulus encoding

Many neurons (overall 35.7 %) in vINCL varied their firing rate significantly according to the color identity to one or several locations during different task periods. We found the largest proportion with nearly half of the population of vINCL neurons (46.9 %), showing selectivity for color identity during the sample phase. The proportion of sample-selective neurons with a high color information in the vINCL is reminiscent of previous findings in crows (31-46 %)(Moll & Nieder, 2015; Veit et al., 2014) and in monkey PFC neurons during delayed-matching to sample and paired association tasks (34-44 %) (G. Rainer et al., 1998; Gregor Rainer et al., 1999; Warden & Miller, 2007).

At the population level for vINCL, selective attention modulates sensory processing during the sample period of the task, to prioritize stimulus information in the service of WM. In this way, the representations of relevant color features of interest are enhanced in favor of the cued location. This action serves at the perceptual level of WM to optimize the use of the capacity limit resources. Selective attention prior to stimulus onset can gather relevant information, and guide a less demanding encoding of the information, as color information for that location is no longer shared between other onscreen locations.

In fact, the color information for no-cue trials, thus without allocation of attention to only one location, has a diminished effect. Without the use of the pre-cue before sample presentation, WM encoding of the colors is affected by how many stimuli are in the array (Buschman & Kastner, 2015). Consistent with our behavioral results, other behavioral studies showed that when attention is distributed over several locations of the visual field, rather than in one, there is a corresponding loss in spatial resolution and processing efficiency for any given location (e.g., Castiello & Umiltà, 1990; Eriksen & Schultz, 1979; Eriksen & St. James, 1986; Shulman & Wilson, 1987). With a fixed number of three stimuli in their left hemifield, crows are playing the task beyond their WM capacity (2-items per hemifield). In fact, the visual hemifield of crows show largely independent capacity, like in monkeys (Balakhonov & Rose, 2017; Buschman et al., 2011). Therefore, in the no-cue condition the color encoding of a specific location is affected by the presence of other two stimuli in the same side as the target (ipsilateral). The target location analysed has now to cope with an increased “distractibility” (Lavie, Hirst, de Fockert, & Viding, 2004), and the lower color information carried by the neuron correlates with the behavioral impair in no-cue trials (Eriksen and Eriksen, 1974). The no-cue compared with the pre-cue condition reveals that the color trace for a particular location

contains less information during encoding, due to irrelevant information overloading a limited memory capacity (Vogel, McCollough, et al., 2005).

The WM resources are now divided to split the focus of attention between all the three stimuli on the screen in order to extend enough color information for each representation and ensure the detection of the change. As seen in lateral PFC, the neuronal response amplitudes in vLNCL decrease with increasing numbers of stimuli to maintain (Buschman et al., 2011; Keitel, Andersen, Quigley, & Müller, 2013; Moran & Desimone, 1985). When two items were presented as memoranda within the same visual hemifield, the stimulus selectivity of prefrontal neurons was significantly attenuated, suggesting that the limited capacity of WM is the result of the limited computational capacity of single neurons (Funahashi, 2017).

The attentional mechanisms involved in WM contents are confirmed by a low resolution of color information for irrelevant locations in the presence of a pre-cue in a different location. In this case, selective attention diminishes the color representations for those stimuli that are not relevant for the goal. In pre-cue trials the color information for locations without a pre-cue is close to baseline. The WM contents are suppressed to optimize those of the relevant location (Zanto & Gazzaley, 2009). Those results are confirmed with the population analysis exclusive for selective sensory-cells, demonstrating a strong tuning for the color information in all the relevant locations, with a particularly high effect on the pre-cue location. Consistent with previous studies in humans and monkeys, attentional mechanisms operate upon the perceptual and WM representations optimizing the use of the limited capacity storage by enhancing the color information from relevant locations, while diminishing the color representations of the less relevant (Carrasco, 2011; Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006).

Delay period analysis: stimulus maintenance

To demonstrate that the encoding is not the end point of selective attention (Gazzaley, 2011), we analysed the effect of attentional cue on color information during the delay, where the color information is maintained. Typically, neurons contributing to WM hold modality-specific information online over a delay (Hains & Arnsten, 2009). We found color-selective neurons during the delay period. In vLNCL, the proportion of sensory-related neurons in the delay (34.7 %) is consistent with previous findings in crows (19 %-31 %) (Moll & Nieder, 2015; Veit et al., 2014) and in monkey prefrontal neurons (30 %)(Vallentin & Nieder, 2010). Comparable selectivity was also found in

pigeons (21-67 %), although most task designs do not allow one to disentangle the reward prediction and motor components of the task (Browning et al., 2011; Diekamp et al., 2002; Milmine, Watanabe, & Colombo, 2008; Moll & Nieder, 2015; Rose & Colombo, 2005). Curiously, a high fraction of visual responsive cells in the sample period (44.8 %) exhibits the same color selectivity in the delay period. This indicates that nearly half of the visual responsive cells represents color information in the delay, besides the presence of a bigger fraction of new cells with delay activity present specifically in the delay. This is visible at the population analysis restricted by significant cells, which strengthen the color information in the early delay, after sample offset. The vINCL population exploits the focus of attention to continue operating during WM maintenance to favor the color information in WM (Awh, Vogel, & Oh, 2006; Awh & Jonides, 2001; Gazzaley, 2011). Similarly to the encoding phase, the pre-cue enhanced the strength of the neural color contents in WM compared to no-cue trials and to the irrelevant locations. According to attentional mechanisms on the perceptual domain (the encoding)(Lepsien and Nobre, 2006; D'Esposito et al., 2000; Gazzaley, 2011; McCarthy, 1995), the functional support of attention in WM maintenance shows an analogous pattern of modulation and suppress the irrelevant color information.

Comparison period analysis: stimulus retrieval and encoding of new stimuli for comparison.

At this last part of the task, thanks to a control no-go period between the comparison presentation and the choice, it is possible to analyse the retrieval phase of WM without movements artifacts. The comparison period allows us to examine whether the retrieval process is influenced by similar mechanisms of attention (Gazzaley, 2011). A small fraction of the vINCL population showed color-selectivity during the comparison period (21,6 %). Within this fraction only 10.6 % shared this selectivity during both the sample and comparison periods and 13.5 % between the delay and choice, underlying specific new cells to sustain a memory characteristic of retrieval activity. Overall, the vINCL population have a small effect in reactivating the color information in the comparison. The higher color contents revealed in pre-cue conditions in the encoding and maintenance stages, does not enhance the retrieval, demonstrating that the mechanisms of recall of color information are efficient in both pre and no-cue locations during correct trials. Importantly, the modulatory pattern for pre-cue and no-cue locations remains significantly separated from the irrelevant locations.

Moreover, in this last phase of the task, free from movement artifacts, it is possible to separate the retrieval of the colors presented in the sample, from the parallel encoding effects of the new comparison-colors. As in the encoding of the sample-array, many neurons show color-selectivity for the comparison-array (39.7 %). The analysis from the encoding of the new comparison stimuli show in this phase, an identical effect previously seen in the encoding stage of the sample-array, such that the pre-cue locations have a robust color content compared to the no-cue locations. Moreover, the irrelevant locations are not considered in the perceptual process of a new color. Again, mechanisms of attention provide a means to specify what will be or not represented based on the task-goals (Desimone & Duncan, 1995). Attention profitably facilitates the rearrangement of the WM resources enhancing the color information for the incoming decision.

Comparison period as decision-making

The two parallel processes of WM of retrieval and encoding can be combined to access the effect in the detection of the change in the comparison period. The change detection analysis can interface mnemonic representations from the sample-array and the new perceptual stimuli from the new comparison-array, affecting equally the neural responses. During the comparison period, the change detection information has a high effect in both pre and no-cue conditions, right after the comparison-array. This effect reaches the maximum effect exactly when the birds are allowed to make their decision, addressing the involvement of vINCL neurons in the decision and choice, This is a similarity with FEF neurons, which exhibit an increase in activity interpreted to enhances the perceptual representations in visual areas and ultimately improve the accuracy of the required decision (Zhou & Thomson, 2009; van der Togt et al., 2016).

As expected, the change detection of a color is strong in the period of the task in which the bird needs to retrieve and compare the colors at the relevant locations. This is in accordance with a comparable retrieval efficiency in correct trials of the color information in both pre- and no-cue locations on the comparison period to grant the right detection. However, the neuronal results contrast with the behavioral accuracy, in which both birds significantly benefited from the pre-cue trials in the change detection. The pre-cue does not affect the neural response increasing the detection effect, even constraining the detection at only one location. Another explanation could be that this effect is driven by motor preparatory activities of vINCL neurons that direct the movement of the response.

This could support the “premotor theory of attention” of regions like FEF and LIP (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). The link of change detection with decision-making could give an important role on vINCL on the action selection, a role often covered by PFC and PPC (Ding & Hikosaka, 2006; Louie, Glimcher, & Webb, 2015; Sugrue, Corrado, & Newsome, 2004). The sensorimotor role of vINCL in selecting between competing motor actions is peaking right after the comparison-array offset, where most of the single-cells have a characteristic inhibitory effect on the firing rates. This suppression activity could serve to the birds to restrain the impulse to answer and to wait the exact response interval of the task.

Location information processing

Aware of the advantages of using the pre-cue, the birds understood the importance to discriminate between pre-cue and no-cue trials to play efficiently the task.

The vINCL neurons detect successfully the presence of spatial cues. The effect of cue is particularly high at the pre-cue onset. After the cue offset, the effect decreases and stabilizes from the sample to the entire delay. The cue presence triggers an efficient “alerting” strategy of attention not only in the pre-encoding phase but also in the most critical aspect of WM, the maintenance. Attention in vINCL maintains a state of high sensitivity to incoming stimuli to test, a mechanism associated with the frontal and parietal regions in humans (Marrocco & Davidson, 1998). Sustained activity in higher order areas prior to stimulus presentation (sample- and comparison-array) could be a neural substrate of an attention selection signal (Lara & Wallis, 2015).

Furthermore, the location information carried by pre-cue items confirms the attentional control benefits on WM in the task. Specifically, the pre-cue enhances the location information compared to the no-cue condition which stays as expected at baseline, since the sample-array placed at the same locations. Neurons in vINCL enhance the representations of the relevant location to maintain when spatially pre-allocated by attention. The modulation is driven by the pre-cue presentation in the beginning of the trial. Such spatial relevance in vINCL neurons in the pre-encoding phase of the stimulus could represent the control mechanism that selectively orient attention to a specific location, as seen from a fronto-parietal attention network (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Corbetta & Shulman, 2002; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). Like in McNab et al. (McNab & Klingberg, 2008), a greater activity in PFC during pre-

encoding expectation period is enable in establishing a filter that prepares and focuses encoding resources. A similar effect is seen in vINCL, involved in the selection of relevant spatial information that goes into WM. Attention mechanisms not only enable crows to gather relevant information from the sample, but it also maintain the task goal (Carrasco, 2011), favoring the spatial representation within the entire delay, thus within WM, for the comparison. In pre-cue trials, the vINCL neurons maintain sustained location information even without the presence of any stimuli, until the comparison period. This effect correlates with improved behavioral performance, and previous color information analysis, such that when attention is turned toward a specific location, the color information of vINCL neurons increases. Since this process is driven by cognitive contents, this provides a potential demonstration of the cognitive penetration of perception by attention (Gross, 2017). Our data could show that attention affects perception in a controlled way. That is, the maintenance of the stimulus location could favorite the increase of the stimulus encoding in the comparison. The spatial modulation on each delay phase (after pre-cue and sample presentation) could serve to increases the color sensitivity at that location in WM and to improve consequently the performance. The location information drops dramatically after the comparison-array onset, where all the three locations are present on the screen and the location information is been already bound in the color to detect. The retrieval is not affected by location information, or by the cue presence. The crow's vINCL shows orienting mechanisms of attention characteristic of human posterior brain areas as the superior parietal lobe, the temporal parietal junction and the FEF (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Posner, 1980).

The mNCL

Interestingly, in mNCL, fewer cells were stimulus-selective than compared to the vINCL. Unlike the vINCL region, at singular level (Fig. 11), the presence of a stimulus-selectivity does not seem to show a defined firing rate modulation split by the task conditions, confirmed by a high overlap of significant neurons between task context and periods. The firing rate of vINCL cells show a persistent activity during the entire trial, regardless of the stimulus properties. Because of a persistent activity even during the ITI, we disproved potential similarities with “fixation cells” found in the dorsolateral PFC, with a puzzle role in attention and eye movements (Sun et al., 2017; Zhou & Constantinidis, 2017).

The mNCL population do not show a distinct pattern of relevant WM contents between the pre-, no-cue and irrelevant locations. Concerning a lack of color and location information in the entire population, this area may not be important for the processing of the visual information. Indeed, the mNCL could be involved in the process of auditory information as caudal medial nidopallium (NCM). In literature, NCM is a higher order auditory area (Soyman & Vicario, 2017) and for this reason, further investigations have to be done under the use of auditory stimuli.

From our convergent results derived from two areas of the NCL (vINCL and mNCL), we conveyed two different neuronal populations. Within the vINCL, a balanced fraction of the populations showed a purely visual response independent of the task-context, thus of the sample- and of the comparison-arrays, a purely memory response in the delay and also an intermix response that carry the visual response in the related delay. The multi-selectivity advantage of different response properties found in vINCL lays in a behavioral flexibility of the area to support task performance. The influence of vINCL by different stimulus features is another similarity with a mix cognitive factors selectivity of PFC neurons (Raposo, Kaufman, & Churchland, 2014; Rigotti et al., 2013). This is confirmed by the lack of context dependent selective neurons in mNCL. In this area, the neural representation of the sample stimulus do not differentiate between the conditions or the task information throughout the trial, showing indeed more interdependency between the different task periods.

Interestingly, in both vINCL and mNCL areas, a major fraction of neurons show a significant color information in location 1. The commonality of those areas could be the AP location of recordings, speculating the presence of a topographic map of visual space, which can represent in WM precise locations of the stimulus position in the screen, like the mammalian FEF and IPS (Hagler and Sereno, 2006; Silver and Kastner, 2009; Wang et al., 2014).

Conclusion

Taken together, our data demonstrates neuronal correlate of attention on WM contents for color and location in the avian vINCL. Through vINCL, crows were able to actively retain information modulating the neuronal response in WM for location and color features of the relevant

stimuli. The effects of selective attention on the magnitude and coherence of perceptual representations in the vNCL, were similar to those imply in prefrontal and parietal networks, confirming the involvement of this area in the WM system. The absence of a strict dichotomy between purely sensory neurons and purely delay neurons, depict the same complicating analysis of the effects of attention in the mammalian higher-order cortical areas (Yantis, 2008).

The deployment of attention in vNCL activity through spatial-cues allows crows to optimize performance and accuracy in a change detection tasks most probably because at the neural level there is an increase of the neural contents for color and location information carried in WM on the cued locations. Moreover, attention allows the crows to optimize the capacity limits by enhancing the neural contents of color and location features of the relevant information, while suppressing the irrelevant information (Knight, Staines, Swick, & Chao, 1999; Neill, Valdes, & Terry, 1995). The vNCL is influenced by attentional mechanisms that dynamically modulate neuronal excitability during selective encoding of items to be remembered and in the retrieval and comparison, as well as in the absence of external stimuli during maintenance of items in the temporal delay. The neuronal population successfully carried the color and location information through the sample and delay until the comparison period where the new color of the relevant location is boosted for a better detection, meaning that attention processes are controlled in the service of WM goals (Gazzaley, 2011). Oppositely, this attentional modulation was not present in the mNCL: this area was not engaged in WM processes under the visual domain. Taken together, our findings could elucidate the neural mechanisms by which information held in WM benefits from selective attention in crows.

Those findings in the avian model contribute to the human literature describing attention as an active modulator of perceptual computations that is able to act at many different levels of the information processing (Macpherson, 2015; Nanay, 2015; Noudoost, Chang, Steinmetz, & Moore, 2010; John H. Reynolds & Chelazzi, 2004).

A further electrophysiological analysis of the local-field potential is possible in this task, since we recorded low frequencies both NCL sites. This analysis could reveal the presence in birds of gamma oscillation during mechanisms of attention and WM, as previously seen often been associated with stimulus processing in monkeys' PFC (Fries, Reynolds, Rorie, & Desimone, 2001; Lundqvist et al., 2016). The combination of two multi-channels electrodes could test patterns of communications between different NCL areas.

Future electrophysiological recordings in crows vINCL could include the presence of invalid precues to overcome the “limits” of error trials analysis resulted by the optimal performance of the crows. Moreover, the presence of distractors before the probe-array could lead to a more challenging task for our crows and testing inhibitory mechanism of attention in vINCL. Nevertheless, other studies need to establish the role on WM and attention of mNCL, especially involving an auditory component in the WM task.

CHAPTER 3:

Executive control over working memory in crows.

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Abstract

Executive control is a cognitive process that controls and modulates goal-directed behavior. Many studies demonstrate that corvid birds exhibit a remarkable cognitive range of human abilities that necessitate cognitive processes to act in a controlled and supervised way. Despite these abilities, in crow remains unexplored an executive control action during a WM task.

Here, crows have to make flexible and profitable decisions between four reward magnitudes contingently associated with four locations. Two crows (*Corvus corone*) performed in touchscreen-equipped operant chambers a delayed-matching to location task to optimize the reward magnitudes. Asked to choose the higher reward relative to the other, the crows show a flexible control over the information processing resulting in accurate and fast response towards conditions that had been paired with higher-reward magnitudes. Following a distance effect, the reward discriminability seems more effective increasing the difference between reward magnitudes. These results show that crows, like humans, evolved a flexible control of on a WM task, triggering fast and accurate responses when involved more beneficial reward magnitudes.

Keywords:

executive control, working memory, crows, delay-matching to location task, reward magnitudes.

Introduction

Working memory (WM) is the ability to maintain and process information during the execution of cognitive tasks (Cowan, 2014). It is a limited storage system that keeps information actively at the service of other cognitive processes involved in carrying out a task. Given the limited capacity of WM, it is crucial to control what information is maintained for the current behavior. For instance, imagine an animal that has just encoded information about the locations of different food items varying in magnitude. Depending on its position in rank order, it might be beneficial to focus on the location of the lower-magnitude food, in case a higher-ranking animal is present as well. Thus, by allocating WM resources to the information concerning the position of the lower-magnitude food, the animal can increase its chances to retrieve food without risking losing it to the dominant animal. The benefit in this case relies on the proficiency which this animal keeps available information for maintenance and retrieval, based on the current behavior (Brady & Hampton, 2018). For this reason, WM is fundamental not only as an informational storage but also as an executive control (Miller et al., 2018). This is only one example of how the “executive control” gained a relevant place in many WM models (Baddeley & Hitch, 1974; Cowan, 2005; Miller & Cohen, 2001; Miller et al., 2018).

The term “executive control” refers to a cluster of cognitive processes that control and modulate goal-directed behavior (e.g., Olson & Luciana, 2008; Shimamura, 2000; Traverso, Viterbori, & Usai, 2015). It is a higher-level control system that governs the information processing. For instance, the executive control enables the WM system to selectively attend to some stimuli and ignore others. It can shift, update and inhibit information in WM (Arbuthnott & Campbell, 2000; Dempster & Corkill, 1999; Miyake et al., 2000; Morris & Jones, 1990; Shilling et al., 2002; Smith & Jonides, 1997).

In recent research, corvids (crows, jays, ravens, and jackdaws) have repeatedly demonstrated their complex cognitive abilities (Emery & Clayton, 2004), as signs of executive control (Barrigar, 2017). Abilities such as analogical reasoning (Smirnova, Zorina, Obozova, & Wasserman, 2015), episodic-like memory (Clayton & Dickinson, 1998; Raby, Alexis, Dickinson, & Clayton, 2007), tool use (Hunt, 1996; Knaebe et al., 2017; Lambert et al., 2017; St Clair & Rutz, 2013; Weir, 2002), complex social interactions (Bugnyar, Reber, & Buckner, 2016; Massen, Pašukonis, Schmidt, & Bugnyar, 2014; Massen, Ritter, & Bugnyar, 2015), mirror self (Medina, Taylor, Hunt, & Gray,

2011), insight into the mental state of conspecifics (Clayton et al., 2007), motor self-regulation (Kabadayi, Taylor, Bayern, & Osvath, 2016) and a high WM capacity (Balakhonov & Rose, 2017) demand the activation of different cognitive processes in a controlled and supervised way to be successfully executed.

Despite crows abilities in solving sophisticated tasks (Auersperg et al., 2011; Kabadayi & Osvath, 2017; Logan et al., 2014; A. H. Taylor et al., 2009; Alex H. Taylor et al., 2011), the executive control of WM remains unexplored in crows.

Most behavioral paradigms used in animal research only tap into distinct parts of WM and, most of them, have already been used in crows. Delayed-matching to sample and similar variation of WM tasks (Balakhonov & Rose, 2017; Ditz et al., 2018; Ditz & Nieder, 2016; Goto & Watanabe, 2009; Moll & Nieder, 2015; Veit et al., 2014) are widely used to test visual WM and WM capacity in animals. The Aesop's Fable paradigm (Logan et al., 2014), instead, investigates causal understanding, the process of identifying the relationship between a cause and its effect. The food-caching paradigm (Clayton et al., 2007) is used to study spatial WM and the string-pulling paradigm (Heinrich & Bugnyar, 2005; Taylor et al., 2010) tests spontaneous problem solving (Jacobs & Osvath, 2015).

The executive control is proposed to act on WM as an integrative modulator among several options competing for the current behavior (Anderson, 2002). Therefore, it is challenging to test its contribution in an operant chamber, which would increase research standards and comparative utility. The lack of an accurate executive control paradigm lies on the difficulties to incorporate more complex life-like challenges within performance measures (Burgess, Alderman, Evans, Emslie, & Wilson, 1998; Chan et al., 2008; Shallice & Burgess, 1991).

To fully challenge executive control in a WM task, we presented two carrion crows with a novel paradigm that incorporated elements from delayed-matching to sample, spatial WM and differential outcome discrimination tasks. The task was a delayed matching-to-location (DMTL), modeled for assessing executive control mechanisms with different reward-magnitudes associated to spatial WM. The DMTL task contained four possible spatial cues and four possible remember cues. Each remember cue was associated with a specific magnitude of reward. The different reward-magnitudes linked unique outcomes to each stimulus (Hochhalter & Joseph, 2001). Pre-established the reward magnitudes of each remember cues, in the actual DMTL task, the crows had to remember four cues in each trial, two spatial and two remember cues. Thus, the memory load of each trial was

at the maximum of crows WM capacity, estimated to be at about four items (Balakhonov & Rose, 2017). This DMTL task required short-term memory storage of several pieces of information through a dynamic integration: the magnitude of the reward had to be abstractly transferred from the remember cue to the spatial cue. The remember cue instructed the animal on the reward magnitude associated with the preceding location. Each spatial cue gained a different and contingent meaning in each trial, due to the variable association with the remember cues. In the end, the birds had to select the spatial cue that was associated with the most favorable reward magnitude.

The executive control governs the task between more beneficial stimulus associations, through discrimination and comparison processes. In order to succeed the trial, our crows had to associate reward and spatial information, maintain multiple items in WM under control to protect it against distractors or discharge it to obtain the reward, and in the end, make a decision based on the mnemonic information.

Further, testing executive control in an operant chamber has numerous analytic advantages over maze or more general open-space procedures in terms of more precise control of timing and behaviors. Learning in these settings is better suited to examining discrete trials or episodes of behavior. The combined setup with a head-tracking system ensures the fixation position of the subject during stimulus presentation and allows us controlling specific variables of its behavior; for instance to prevent undesired behavioral strategies and to include only voluntarily attempted trials. Those task conditions and the task per se promote the reproducibility within the subjects and it represents a competitive paradigm for executive control of WM adaptable to comparison studies.

Since crows have already succeeded in many of the individual paradigms involved on this project, like spatial WM and delayed-matching to sample tasks, our experimental assumption is that they are capable to executively control information held in WM in a fully controlled experimental setup.

Materials and Methods

Subjects

Two hand raised male carrion crows (*Corvus corone*) of 10 months of age, with baseline weights of 490 and 460 g, were used in the current experiment. The crows were housed in social groups of four birds in an aviary with a twelve hours day/night cycle. During training and behavioral testing water and grit was kept unrestricted but they were maintained on a controlled food protocol such that food-pellets (Nutribird F16, Versele-Laga, Germany) could be used as a reward during each training session. The pellet was delivered into a small feeding trough and illuminated during the reward-period. The animal's body weight was controlled daily. When not in experiments, the crows were given food *ad libitum*. All preparations and procedures were performed according to the principles of the care and use of laboratory-animals adopted by the German Animal Welfare Law for the prevention of cruelty to animals and were conducted after approval by the LANUV (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen).

Experimental setup

The setup consisted of a chamber (50 cm (width) x 50.5 cm (depth) x 77.5 cm (height)), equipped with a camera used for remote monitoring and feedback (Sygonix, Taiwan), and a custom-made automatic pellet feeder (plans available: www.jonasrose.net). The bird was placed on a wooden perch in front of a 22" touchscreen (ELO 2200L APR, Elo Touch Solutions, Inc) such that the maximum distance from the bird's eye to the screen was 7 cm. The animal's head position was tracked in the horizontal, including the rotational angle of the head, with an open-source computer-vision camera 'FLIR' (Chameleon3, Point Grey Research Inc., Richmond, BC, Canada). A lightweight 3d-printed reflector was mounted on a lightweight surgically implanted head-post for head-tracking and removed after each experimental session. During the training, the reflector was detected by the camera to report location and angle of the crows' head. The frame rate of the camera was 150 Hz and data were smoothed by integrating over 2 frames in Matlab using custom programs on a control PC. All aspects of the experiments were controlled by custom programs in Matlab using the Biopsychology (Rose, Otto, & Dittrich, 2008) and Psychophysics toolbox (Brainard, 1997).

Behavioral protocol

The crows were trained on a DMTL task (Fig. 15), modeled for assessing executive control of spatial WM depending on different reward magnitudes. Each bird was tested daily. During experimental sessions, periodically brief breaks with access to water were offered to the animals.

Trials began with a 4000 ms inter-trial interval (ITI). Following the ITI, crows were presented a white fixation dot in the center of the screen (maximal 5000 ms). To initiate and to complete a trial, the crows had to hold their head still (less than ± 2 cm horizontal or vertical displacement) and look straight at the fixation dot on the screen (less than $\pm 17^\circ$ horizontal or vertical rotation). Moving their head before the response period resulted in an aborted trial. Once the crows fixated the dot, a sequence of cue presentations followed. In the sequence, two spatial cues (white squares) were presented for 300 ms at randomized positions out of four possible screen-locations, at each corner of the screen (L1, L2, L3, L4), each interrupted by 600 ms delay-period (D1 and D3). Following each spatial cue and the corresponding delay, a remember cue (a colored ring) appeared in the center of the screen for 300 ms instructing the animals on the reward magnitude to gain on the preceding location. Four remember cues were used, each with a unique reward magnitude: reward 0 (R0) meant no reward, R1, R2 and R3 indicated one, two or three pellets, respectively ($R3 > R2 > R1 > R0$). Each remember cue was followed by a 600 ms delay (D2 and D4).

Only after the entire sequence was displayed, the two spatial cues previously presented were simultaneously available. The spatial cues indicated the amount of reward associated with the remember cues in that trial. At this point the crow was required to move its head and make a single peck to one spatial cue. In order to obtain a reward, the animal had to choose the spatial cue associated with the higher reward magnitude.

An incorrect response, a peck at the spatial cue associated with the lower reward magnitude, or a failure to respond (within 2500 ms), was mildly punished by briefly flashing the screen white and giving a short time-out (9000 ms). As reward, the pellet (Nutribird F16) was delivered to a little holder on the automated feeder which was illuminated during reward-delivery (2000 ms). Sequences of spatial and remember cues were randomized and balanced across trials. Each bird was assigned with the inverse set of colors of the remember cues.

The spatial cues were white squares, 16.2 degrees of visual angle (DVA) on either side and placed 18.9 DVA above/below the meridian at a distance from the center of 16.2 DVA (center of the stimulus). The remember cues were colored circles, 49.8 DVA placed on the center of the screen (center

of the stimulus). The maximal binocular overlap for carrion crows is around 37.6 DVA (Troszianko et al., 2012); all spatial cues were placed outside the binocular area, including extremely limited range of head rotation and head and eye movement.

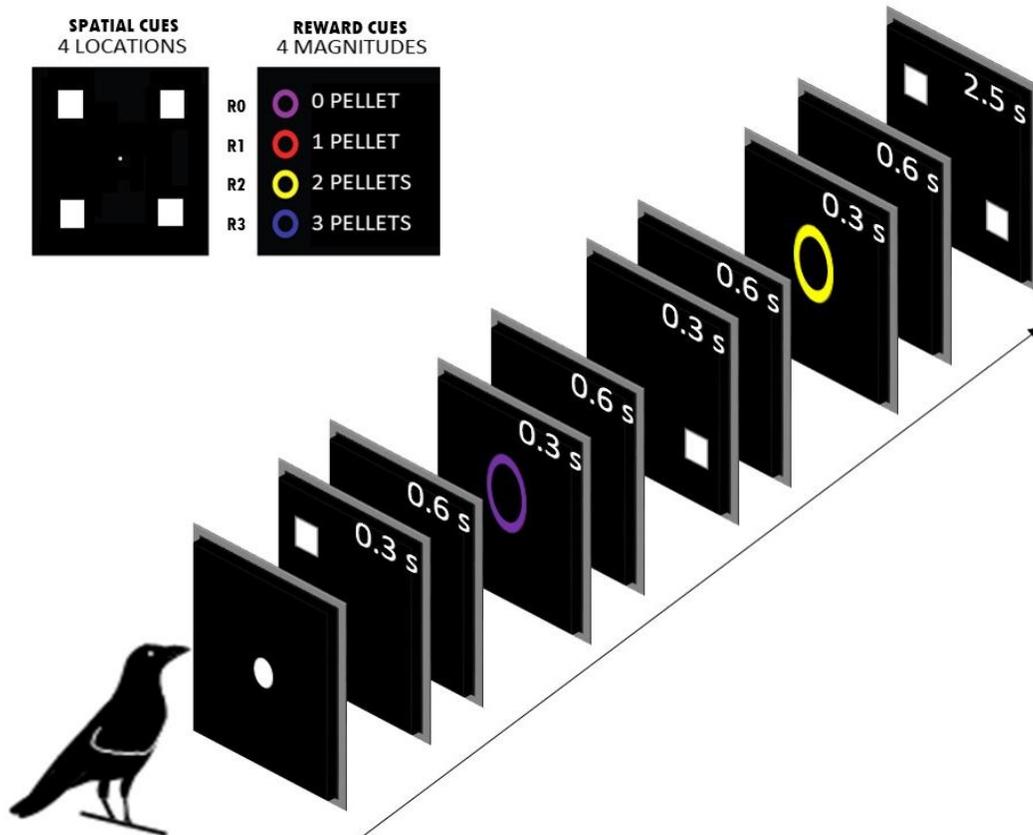


Figure 15. Behavioral protocol: the delayed matching to location task.

To initiate and to complete each trial, the crows had to hold their head straight at the white dot on the screen. Once the crows fixated the dot, there was a sequence of cue presentations where two spatial cues (a white square) was presented for 0.3 s at randomized positions from four possible locations, interrupted by 0.6 s delay-periods. Following each spatial cue and the corresponding delay, a remember cue (a colored ring) appeared in the center of the screen for 0.3 s instructing the crows on the reward magnitude to gain on the preceding location. Four remember cues (R) were used, each with a unique reward from 0 to 3 pellets. After the entire sequence, the two spatial cues previously presented were simultaneously available. The spatial cues indicated the amount of reward associated with the remember cues in that trial. To obtain a reward, the crow had to choose the spatial cue associated with the highest reward magnitude.

Data analysis

Data was collected and analysed with Matlab (Mathworks inc. Natick, MA) using custom code and the statistics toolbox. Data analyses were based on attempted trials only, excluding gaze-breaks trials. Thus, only trials in which the birds acquired gaze fixation and remained still until making an either correct or incorrect response were used for analysis. The effect of the remember cue on performance, gaze-breaks, reaction time for correct and incorrect responses and the Inverse Efficiency Score (IES) were assessed using analysis of variance ANOVA with remember cues combination (reward pair) as single, continuous factor across days. In addition, the effect of the reward pair combination on performance was tested with a binomial test for each animal independently. ANOVA was conducted for each animal independently, followed by Tukey-Kramer Honestly Significant Different (HSD) post-hoc analysis.

Surgery

All surgeries were performed under aseptic procedures. For the head tracking system, a lightweight head-post was chronically implanted to position a small silver colored reflector during behavioral experiments. Before surgery, anesthesia was induced by a mixture of ketamine (60 mg / kg) and xylazine (6 mg / kg) and maintained by endotracheal intubation under isoflurane (0.4 L minute, delivered concentration 0.5-1.5 %). Once deeply anaesthetized, animals were placed in a stereotaxic frame. Few feathers were plucked over the base of the beak exposing skin for a small incision to retract the skin. A small opening was drilled in the surface of the bone in order to expose the *trabeculae* to which the head-post was attached with dental acrylic. The wound-margins were sutured, the anesthetic gas was turned off, and the bird was allowed to breathe pure oxygen for approximately one minute. The endotracheal tube was removed as the bird regained consciousness. The animal was placed in a recovery-cage until fully recovered following the administration of analgesia (morphasol, 3 ml / kg).

Results

Two naïve hand raised crows (*Corvus corone*) were trained on a DMTL, a behavioral task for assessing spatial WM on differential outcomes. The crows were trained for approximately 25 months, after which they were tested for ten consecutive days. Here, we reported the results of those final ten days.

Both birds, COL and FRK performed an average of 645 trials per session (mean \pm SEM, COL: 689 ± 34.15 ; FRK: 600.80 ± 30.32). They successfully learned to choose the spatial cues associated with the higher reward magnitude with an average performance of 80.2 % correct responses. Performing at 81.81 % correct FRK was significantly better than COL at 78.76 % (Fig. 16A; COL: $78.76 \% \pm 1.23$; FRK: $81.81 \% \pm 1.82$; ANOVA: $F(1, 216) = 7.77, p < .001$).

To examine the performance for each reward pair combination, we did a one-way ANOVA with reward pairs as groups. Both crows showed a significantly different percent correct (PC) depending on the reward pairs (Fig. 16B, ANOVA COL: $F(11,108) = 43.59, p < .001$; FRK: $F(11,108) = 30.80, p < .001$). A post-hoc test revealed that the difference in both birds was driven by a performance at chance level for the reward pairs R0 vs R1 (R0, R1: COL: $M = 51.32 \% SD = 2.26$, FRK: $M = 39.97 \% SD = 3.04$), and R1 and R0 (COL: $M = 50.00 \% SD = 2.26$, FRK: $M = 55.81 \% SD = 3.04$). A binomial test for the percent correct of reward pairs confirmed the difficulties in discriminating R0 and R1 (binomial test COL: $p = .48$; FRK: $p = .99$) although for FRK R1 presented before R0 resulted in a performance slightly better than chance, $M = 55.81 \% SD = 3.04$ (binomial test COL: $p = .41$; FRK: $p = .03$).

An ANOVA of response latencies showed that the reaction times significantly differed between the reward pairs (Fig. 16C, ANOVA COL: $F(11,108) = 65.63, p < .001$; FRK: $F(11,108) = 20.09, p < .001$). The reaction time in correct trials with the color pair R0 vs R1 was significantly higher compared to the other pairs (post-hoc test: R0 and R1 (COL: $M = 1118 \text{ ms } SD = 19$; FRK: $M = 806 \text{ ms } SD = 24$), and R1 and R0 (COL: $M = 1139 \text{ ms } SD = 13$; FRK: $M = 787 \text{ ms } SD = 11$)). The reaction time of correct responses were significantly faster compared to incorrect responses for each reward pairs (correct responses: COL: $632 \pm 25 \text{ ms}$; FRK: $509 \pm 22 \text{ ms}$; incorrect responses: COL: $868 \pm 70 \text{ ms}$; FRK: $736 \pm 71 \text{ ms}$; ANOVA: COL: $F(1,108) = 31.97, p < .001$; FRK: $F(1,108) = 19.14, p < .001$) except for the reaction time in trials with the smaller reward pairs (post-hoc test:

R0 and R1 (COL: M = 1118 ms SD = 19; FRK: M = 806 ms SD = 24) and R1 and R0 (COL: M = 1139 ms SD = 13; FRK: M = 787 ms SD = 11)).

The effect of latency and performance on the discrimination ability was quantified using the IES (Bruyer and Brysbaert, 2011). The IES weighs the reaction time against the percent correct and indicates whether both variables were in unison. For each crow, the IES was calculated by dividing reaction time with percent correct of the correct responses in each reward pairs:

$$IES = \frac{\textit{reaction time}}{\textit{percent correct}}$$

The IES values for each reward pair were significantly different (Fig. 16D, ANOVA COL: $F(11,108) = 57.53$, $p < .001$; FRK: $F(11,108) = 32.05$, $p < .001$). However, a post-hoc analysis revealed that only the IES of R0 and R1 pair compared to all other reward pairs was different (post-hoc test: R0 and R1 (COL: M = 2428 ms SD = 1.9; FRK: M = 2144 ms SD = 19) and R1 and R0 (COL: M = 2344 ms SD = 1.7; FRK: M = 1455 ms SD = 14).

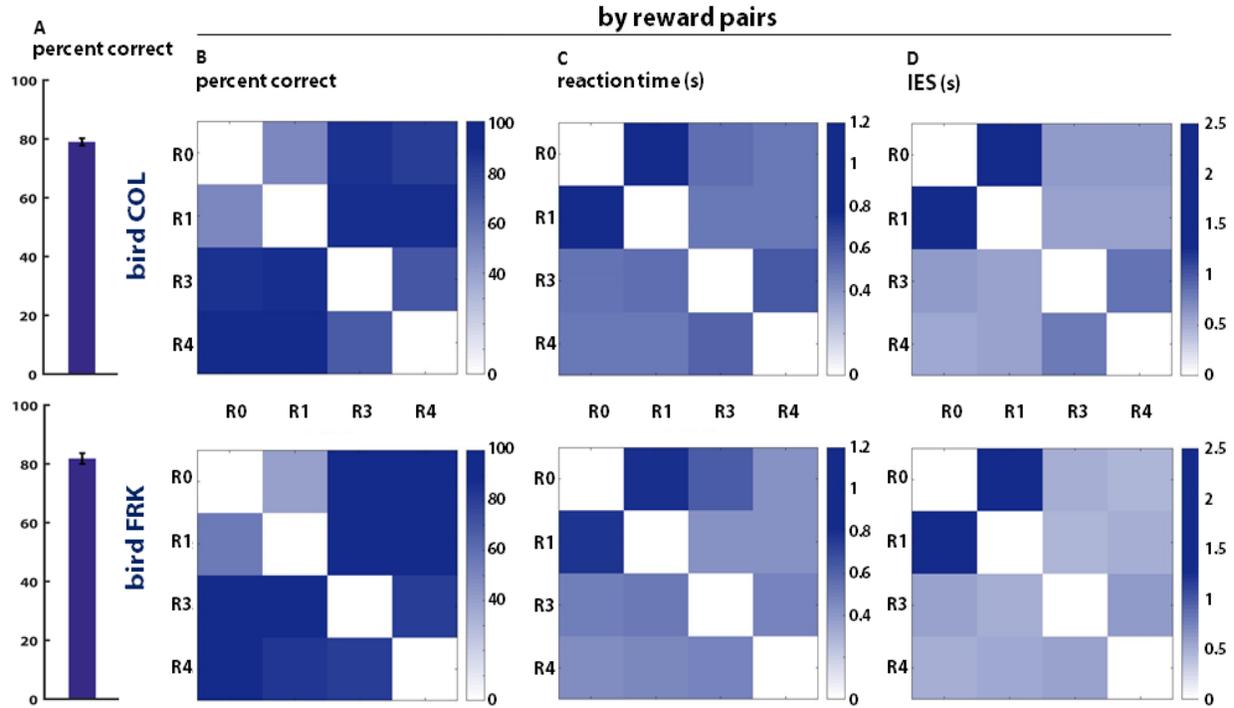


Figure 16. Behavioral measurements.

A) Overall crows performance. Error-bars are SEM. Chance level is 50 %. B) Percent correct of both crows as a function of reward pairs (R0, R1: COL: 51.32 ± 2.26 %, FRK: 39.97 ± 3.04 %; R1,R0: COL: 50.00 ± 2.26 %, FRK: 55.81 ± 3.04 %). C) Reaction times of both crows in correct trials as function of reward pairs: (R0, R1: COL: 1.1 ± 0.01 s; FRK: 0.8 ± 0.02 s; R1, R0: COL: 1.1 ± 0.01 s; FRK: 0.7 ± 0.01 s). D) Inverse Efficiency Score (IES) of both crows as a function of reward pairs: R0, R1: COL: 2.4 ± 1.9 s; FRK: 2.1 ± 0.01 s; R1, R0 (COL: 2.3 ± 0.01 s; FRK: 1.4 ± 0.01 s).

The crows' performance was not dependent on the sequential order of the remember cues that formed the reward pairs (i.e. in trials with R1 as first color the crows showed the same performance as in trials with R1 as second color within the pair R1 and R0), resulting in a symmetrical pattern of performance for each reward pair (no dependency of which remember cue was shown first (ANOVA: COL: $F(1,108) = 11.97$, $p < .11$; FRK: $F(1,108) = 12.19$, $p = .68$). All behavioral parameters (percent correct, reaction time and IES) significantly varied between reward pairs if they were pooled across both sequential orders of pair (e.g. R0 – R1 and R1 – R0) (Fig. 17 A-C; percent correct: COL: $F(5,54) = 185.80$, $p < .001$; FRK: $F(5,54) = 91.68$, $p < .001$; reaction time COL: $F(5,54) = 86.61$, $p < .001$; FRK: $F(5,54) = 43.67$, $p < .001$; IES: COL: $F(5,54) = 141.38$, $p < .001$; FRK: $F(5,54) = 77.33$, $p < .001$), due to R0 vs R1 (post-hoc test percent correct: COL: $M = 50.66$

% SD = 1.13, FRK: M = 47.89 % SD = 1.80; reaction time: COL: M = 1.160 ms SD = 20, FRK: M = 7965 ms SD = 22; IES: COL: M = 2386 ms SD = 6, FRK: M = 1800 ms SD = 59).

Furthermore, we tested if the discrimination performance of different reward pairs indicated a “distance effect” (Goldfarb, Henik, Rubinsten, Bloch-David, & Gertner, 2011). In other words, we tested if the discrimination ability between both remember cues was dependent on the numerical distance between the reward magnitudes to compare, here called “reward step”. For example, the reward pair R0 (no pellet) and R2 (two pellets) had a reward step of two. We split the reward pairs in three difficulty levels: the hardest conditions had a reward step of one; the intermediate had a reward step of two; and the easiest had a reward step of three. Due to the significant different behavioral values of R0 vs R1, we exclude this pair and we performed an ANOVA to test the effect of the reward steps on all the behavioral parameters (Fig. 17 D-F). Percent correct and IES, but not the reaction time, varied between the different reward steps (percent correct: COL: $F(2,27) = 26.18$, $p < .001$; FRK: $F(2,27) = 3.66$, $p = .03$; reaction time COL: $F(2,27) = 2.99$, $p = .07$; FRK: $F(2,27) = 1.24$, $p = .3$; IES: COL: $F(2,27) = 13.03$, $p < .001$; FRK: $F(2,27) = 3.87$, $p = .03$). Both birds had more difficulties in distinguishing trials with a reward step of one (post-hoc test percent correct: COL: M = 79.59 SD = 0.88 FRK: M = 87.13 SD = 1.36; IES: COL: M = 718 ms SD = 22 FRK: M = 533 ms SD = 15).

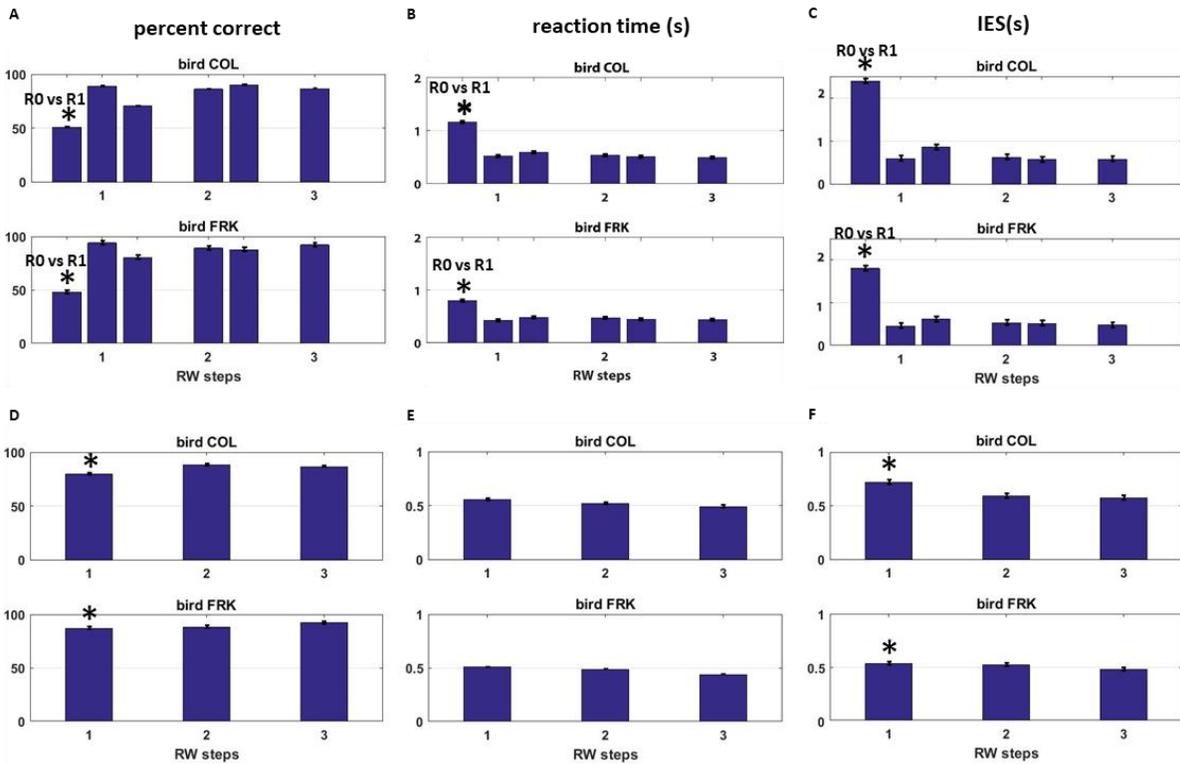


Figure 17. Distance effect.

In the upper part, A) percent correct, B) reaction time and C) IES are pooled across both sequential orders of pairs and divided by reward steps. R0 vs R1 was significantly different. In the lower part without the reward pair R0 vs R1: D) percent correct, F) IES and E) reaction time as a function of reward pairs. Error-bars are SEM.

To determine whether there were any location biases, we analysed the performance depending on spatial cues. Stimuli could be presented at one of four possible locations. There were no preferred locations for crow COL, but one for crow FRK, at the expense of a lower performance on the position 3, $M = 73.32\%$ $SD = 11$ (Fig. 18A, B; ANOVA COL: $F(3,36) = 2.20$, $p = .10$; FRK: $F(3,36) = 12.46$, $p < .001$). However, since the stimuli were presented randomly at four locations this location bias cannot explain the observed performance pattern.

A head-tracking system controlled the gaze-direction of the animals to ensure the maintenance of head fixation and to minimize movement artifacts during stimulus presentation. Further, tracking allowed to prevent any behavioral strategies the birds could use to solve the task differently (e.g. moving their head towards the stimulus location to remember). Throughout a trial and the entire

session, both crows did not show any strategy: there was no gaze-breaks bias to avoid specific combinations (Fig. 18C, D; ANOVA COL: $F(11,108) = 0.78$, $p = .66$; FRK: $F(11,108) = 9.07$, $p = .052$). The number of responses on each combination was balanced, thus arguing against a systematic abortion of specific trial combinations (ANOVA both animals: $F(11,228) = 0.27$, $p = .98$; COL: $F(11,108) = 0.63$, $p = .79$; FRK: $F(11,108) = 1.88$, $p = .052$). Both birds only had few omitted trials within a daily session (COL: $M = 0.22\%$ $SD = 0.01$; FRK: $M = 0.12\%$ $SD = 0.00$).

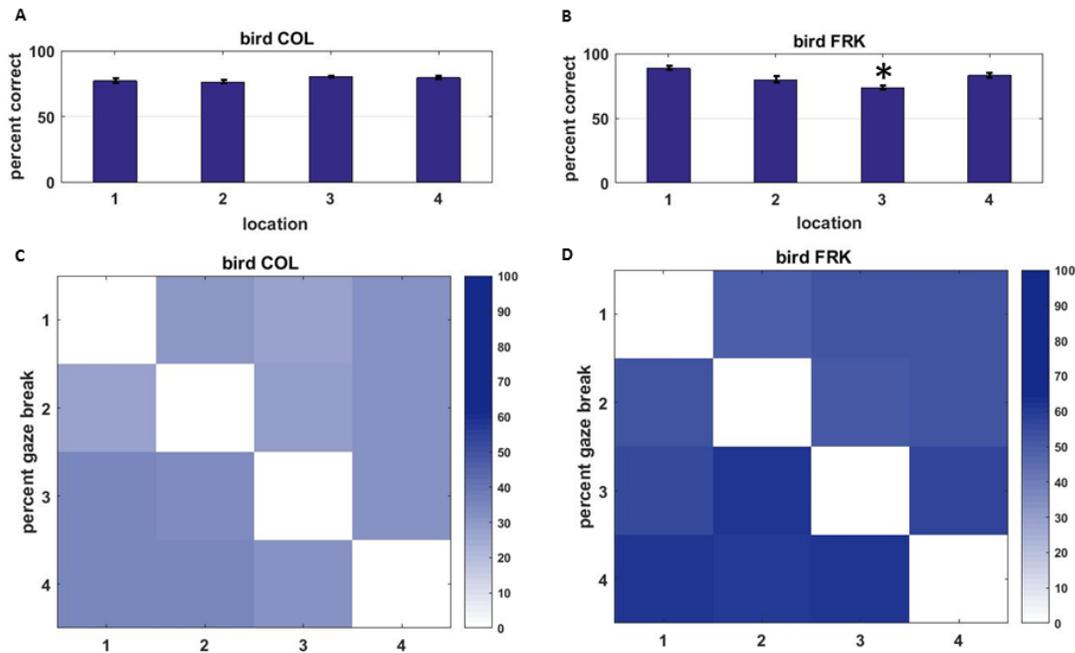


Figure 18. Behavioral bias.

A and B) Percent correct of each crow as a function of stimuli locations (FRK loc3: $73.32\% \pm 11$). C and D) Percent gaze-breaks of both crows as a function of reward pairs.

Discussion

Here we provide critical evidences which indicate that crows have executive control over WM. Crows successfully performed a WM paradigm that included all the components of executive control like maintaining the focus of attention, set shifting, updating WM, and inhibition of irrelevant information (Baddeley, 1986; Logie, 2011; McCabe et al., 2010; Miyake et al., 2000).

Crows demonstrate to work efficiently at their maximum memory load (Balakhonov & Rose, 2017) on a task that involves flexible storing, forgetting and updating of multiple information simultaneously.

In each trial, they had to memorize both spatial cues and the associated reward magnitudes, identify the location that signaled the higher reward magnitude, focus their attention on it and maintain this information in WM until they could make their response. To succeed in this task, they had to suppress sensory input and cognitively inhibit information regarding the irrelevant cues. By actively forgetting the irrelevant spatial cue, they are able to free resources for an active maintenance of the other, important location: a proof of executive control as cognitive flexibility, the ability to quickly and flexibly adapt to changed circumstances (Moore & Malinowski, 2009). The effective executive control of the memory trace during transfer, inhibition and updating of reward information makes an optimal discrimination between reward magnitudes possible. Contrary, an incorrect response, would indicate an erroneous executive control at different levels of the information processing. During this challenging WM task, a deficit in selective attention, interference control or updating of information could be the cause.

In the present study, we developed a new cognitive task that can overcome the limitations in animal research to access executive functions. This task incorporates a representative life-like challenge to test executive control under operant-chamber condition that increase the reproducibility within and across species. The touch screen-equipped operant-chamber allowed installing a head-tracking system to control all behavioral variables. Hence, we could consider only voluntarily attempted trials, avoiding any anticipatory behavior that could reduce the retention interval or any strategy in orienting the beak on the spatial cue.

The different demanding executive functions involved make this task another experiment to add on the corvid cognitive repertoire. The new cognitive evidence lies on the simultaneous occurrence of the mentioned above executive actions to engage control over the WM storage. By successfully performing the task, crows demonstrated a combination of different tasks demands at once: delayed-matching to sample, spatial WM and differential outcomes discrimination. A previous study from Rose and Colombo (2005) already showed that pigeons (*Columba livia*) are capable to control their WM contents in the service of executive functions (see also Kaiser et al., 1997). Pigeons performed a WM task in which cues instructed them whether stimuli should be remembered or forgotten (Rose & Colombo, 2005). Those instructions were reward dependent and did not challenge the WM

maintenance throughout self-control instructions aiming to succeed the trial. By choosing the location associated with the larger magnitude crows are involved in an insightful dynamic control of those instructions: updating and forgetting are mentally rule out by the final goal to facilitate the comparison of the spatial cues.

The task is properly learned by both birds. The behavioral parameters were not affected by the sequential order of the remember cues, indicating that no behavioral strategy was used (i.e. playing the task basing their decision in the first or on the second remember cue to reduce the retention efforts). The bird played the game by paying attention to the entire sequence of cues without aborting any specific reward pair. Moreover, since the reward magnitudes was associated with different colors for each bird, it is unlikely that differences in color discrimination could explain the observed performance pattern. In each trial, the birds retrospectively transferred the information concerning reward magnitude from the remember cue to the spatial cue, thus they generated a within-trial value transfer across stimuli, an ability not new in the avian cognition (Siemann, Delius, Dombrowski, & Daniel, 1996).

Many control mechanisms were involved. In a trial, if the first remember cue was indicating the lowest reward magnitude (R0), the crow was required to forget the associated spatial cue in order to free resources for an active maintenance in favor of the next spatial cue. If, on the contrary, it was signaling the highest reward magnitude (R3), the crow had to stabilize the spatial information and suppress the next stimuli. In case the first remember cue signaled an intermediate reward magnitude (R1 or R2), the crow had to maintain the information concerning both spatial cues as well as their associated reward magnitudes in order to decide correctly. Crows play at their maximum WM capacity, actively maintaining both spatial and remember cues until the choice in which they have to compute all the information to get the reward.

The separated analyses of percent correct and reaction time show that the accuracy is correlated with a faster response. The IES values is in accordance with these findings. The process to compare the reward cues is faster the larger the difference between the magnitudes. In fact, the crows responded correctly and fast in all comparisons except those between the lowest reward magnitudes, where they responded at chance level and slower. Such a behavior is in accordance with an absence of a preference between the smallest reward magnitudes. Indecisiveness and hesitation typically skew the reaction times towards longer latencies during decision-making tasks (Frost & Shows, 1993). This is supported by the very similar reaction time of correct and incorrect responses between

the lowest reward pairs. A similar lack of preference on small reward magnitudes was shown in a discrimination task with pigeons (Siemann et al., 1996). Moreover, an explanation could be given by considering IES as an estimation of the energy used by the bird during the task (Townsend & Ashby, 1983). Under the lowest rewards comparison the crows result to imply a significant higher energy consumption at the expense of efficacy and reactivity.

We could explain this executive effort involved as a consequence of mechanistic difference in attention on that condition. Here, both birds voluntarily do not process the information of the less beneficial cues, preparing an attentional shift to the following or previous stimulus. In other words, the presentation of valueless cues triggers a mechanism of inhibition of the spatial cues associated with those remember cues in WM. This strategic control, effective in all comparisons with the lowest reward magnitudes, does not imply any reallocation of the reward information in any of the two spatial cues associated, at the expense of performance and reactivity. By ignoring remember cues associated with the lowest reward magnitude the crows were able to correctly discriminate between three out of four reward magnitudes.

In agreement with different other studies (Anderson & Reidy, 2012; Della Libera & Chelazzi, 2009; Pessoa, 2009), we validate that pre-established reward association has influences on the spatial allocation of attention. For Engelmann, attention and motivation are tightly modulated by the magnitude of rewards, revealing that motivation can enhance detection sensitivity (Engelmann and Pessoa, 2007). Based on both results, we proposed that increased motivation via food incentives for crows enhances attention, thus maximizing rewards and so performance.

Mechanisms of attention can be triggered by differently valued rewards and result in a prioritization and better WM maintenance of stimuli associated with higher rewards (Kuo et al., 2012; Schmidt et al., 2002; Vogel, Woodman, & Luck, 2005). Our crows successfully learned the reward contingencies with fast reactivity on spatial cues when they were associated to high remember magnitudes (Della Libera & Chelazzi, 2009; Raymond & O'Brien, 2009; Serences et al., 2009). Our results are in line with a recent study by Infanti et al. (2015), in which participants improved performance in a visual-search task when different colors of the stimuli were paired with higher rewards. Crows and humans' memory for neutral items, like for spatial cues in our task, can be modulated by the reward magnitude associated (Infanti et al., 2015).

The reward association generates a preference or a rejection of a stimulus, which becomes clearer as reward magnitudes diverges (Guttman, 1954). Following a distance effect, the stimulus

discriminability seems more effective when the reward step is higher than one: the percent correct and the IES are impaired in the hardest condition in which the crows have to decide based on reward step equal one. Although the optimal performance, the reward step of one, given its small difference, (Gallagher & Alsop, 2001; Godfrey & Davison, 1998; Nevin, Cate, & Alsop, 1993) could conflict with an interference effect of remember cues on spatial cues. In literature, behavioral models of discrimination evaluate stimulus control (the effects of the psychophysical disparity between the stimuli) and reward control (the effects of the consequences for choices) (Alsop & Porritt, 2006). Since each crow had the inverse set of colors for the remember cues, the reward steps of the stimuli are not depending on the stimulus color but on the reward control to compare. To note, that the reaction time does not change between reward steps, suggesting a comparable decoding of the cues information during the choice.

The effect of reward pairs shown in the results extends current knowledge regarding the influence of reward magnitude on WM performance, demonstrating that spatial- reward magnitudes associations tightly interact with costs and benefits of WM (Infanti et al., 2015). Our findings represent a new challenging demonstration of executive control over WM contents of corvids. The level of executive control required in this complex task would be hard to achieve for most mammals, unless the task is fractionated. The analytical power of those results is based on well-arranged paradigms performed in operant chambers that provide very controlled environments. The use of a touchscreen monitor in an operant chamber under head-tracking allows to control online all the responses under stimulus control involved (Nevin et al., 1993). This setup could extend the generality of the findings in assessing executive function paradigms with the precise control of retention and ITI as well as incorporating new measurements of timing and behaviors (Goto & Watanabe, 2009). This work represents a controlled behavioral paradigm for executive control adaptable to comparison studies that can be used for electrophysiological studies. Electrophysiology on the executive control over WM in the avian equivalent of the PFC, the NCL could reveal the neuronal implementation of these complex cognitive processes in birds. It would allow studying the neural substrates of the governing principles between maintenance and forgetting or updating of information. Moreover, investigating neural oscillations in different avian brain areas could show specific patterns of interplay activity in WM between the flexibility and stability of the information during correct and incorrect responses. This task could provide a detailed analysis of the neural processes underlying the selection of reward based-decision under interference. Using the same

memory demand and the same behavioral response, it allows the comparison of neural responses triggered by different remember cues (Leon & Shadlen, 1999). Finally, taking advantage of their human-like cognitive abilities, the use of similar approaches between species will help to compare and understand their behavioral and neural differences and similarities under the 300 million years of independent evolution.

GENERAL DISCUSSION

This part summarizes the main experimental findings and presents a general overview of how our studies in crows can be integrated within the larger context of existing knowledge on WM in human and non-human primates with a particular interest on its interactions with attention and executive control.

1. Summary of the main findings

In my thesis, I investigated control mechanisms of WM as attentional and executive control in crows. The presence of those mechanisms can grant an efficient coordination of memory resources measured as WM capacity, which has already demonstrated to be highly comparable with healthy human and primates (Balakhonov & Rose, 2017).

In the first chapter, we found that crows can use spatial attentional cues to efficiently direct their attention to perceptual stimuli (pre-cue) and on internal representations of stimuli held in WM (retro-cue). By restraining their attention and managing the accessibility of the relevant information, crows mitigated their WM capacity. Importantly, for the first time, we demonstrated the existence of a retro-cue effect in crows. This strongly implies that crows can engage in control over information held in working memory. They were able to improve their memory accuracy and capacity when the stimuli were no longer visible on the screen, but held in WM.

Using the most challenging WM load, 3-colors in one hemifield, the crows played the same task in the second chapter, while recording single-cell activity from an association area, the vLNCL, functionally involved in WM tasks (Ditz & Nieder, 2015, 2016; Moll & Nieder, 2015; Veit et al., 2014, 2015; Veit & Nieder, 2013). Simultaneously to vLNCL, we were the first to record in the recently discovered mNCL (von Eugen, 2017; Sen et al., 2019), in order to elucidate its implication in WM. The task included pre- and no-cue conditions. Cue benefits on the corvid behavior were validated using the same parameters as in the previous chapter: increased percent correct, change detection accuracy and the capacity K.

Neurons in the vNCL modulated their firing rates for specific colors and locations during the sample and the related delay and comparison periods. The selective attention engaged by spatial cues, in the encoding and maintenance of the color, retained more color information when the same location was compared with no-cue location. Attentional mechanisms in WM contents were confirmed by low resolution of color information for irrelevant locations. In this case, the focus of attention suppressed the color representations for those stimuli that were not relevant for the trial. Importantly, in the vNCL mechanisms of attention retained location information within WM, during the delay periods, to later facilitate major color information in the encoding of the sample and comparison color at the cued location. The action of vNCL in the task confirmed the role of the area in higher order cognitive functions. Oppositely, the mNCL was not involved in the processing of visual information. Our data reveal the existence of neuronal correlates of attentional mechanisms upon the perceptual and WM representations in the corvid vNCL.

In the third chapter, we investigated the executive control abilities of crows during a WM task. In order to perform the task, crows had to simultaneously hold in WM multiple items, with color and locations features and their validity. The crows had to retrieve reward magnitudes to memorize spatial information and made a decision over those contents in WM. In the DMTL task, different executive abilities were necessary: it required WM updating, modulation of representations and protection against interferences. The crows' performance revealed ability and limits in controlling the online information in WM, showing efficiency in executive control mechanisms under higher reward magnitudes and a distance effect between the reward magnitudes discriminability.

2. Validation of a corvid model for Working Memory

My thesis describes the concept of WM, the most critical aspect of all the cognitive capacities, such that closely related to fluid intelligence (Salthouse & Pink, 2008), executive function and problem-solving (Cowan, 2014). Indeed, the importance of WM lies in its multiple connections with cognitive operations rather than memory per se. For this reason, it is crucial to study WM in relation to two fundamental aspects, which rule its efficiency and overcome its limited capacity: attention and executive control. Those mechanisms monitor the limited resources and control additional op-

erations like maintaining the focus of attention, set shifting, updating WM and inhibition of irrelevant information (Baddeley, 1986; Cowan, 1999; Engle, 2002; Logie, 2011; McCabe et al., 2010; Miyake et al., 2000). In the past, few studies explored those WM aspects in isolation. In the avian model, attention and executive control, as processes gating WM and modifying its maintenance, have not received much support. Task switching based on rules (Veit & Nieder, 2013) and direct forgetting paradigms (Kendrick et al., 1981; Roper et al., 1995; Rose & Colombo, 2005) have been used to investigate physiologically and behaviorally the avian executive control, in which a cue “instructs” the birds to either remember, forget or change the studied sample. Conceived for electrophysiological studies, those tasks did not challenge the animals to test the accessibility of WM resources and its dynamic control through different memory loads.

Strengthened by the recent demonstration of the existing high WM capacity in crows (Balakhonov & Rose, 2017), the avian model can be repurposed to focus on the processes responsible for this capacity (Amichetti, Stanley, White, & Wingfield, 2013).

In my thesis, I showed that crows performed three challenging WM paradigms that include all the actions of attention and executive control (Baddeley, 1986; Cowan, 1999; Engle, 2002; Logie, 2011; McCabe et al., 2010; Miyake et al., 2000). The crows worked efficiently at their maximum memory load of 4-colors (chapter 3), while flexible storing, forgetting and updating of spatial and reward information simultaneously. They were able to work beyond of that limit (using 6-colors) and to refer to pre and retro-cues for supportive information (chapter 1 and 2). The characterization of similar attention and executive control mechanisms over WM grants the control processes that underlies corvid WM capacity. The way the information is transferred and converted from one form to another (chapter 3), the vigilance for meaningful connections between held information and new solutions (chapter 1 and 3), and the active manipulation through attention (chapter 1 and 2), all those actions play important roles in learning and consequently building their impressive cognitive repertoire.

Here, crows demonstrated impressive examples of WM. They possess retention abilities that rival human beings. Corvids capacity to retain relevant information, continuously update it, and use it to shape behavior towards the present task goal, provide an important research framework to study human memory dysfunctions. Disorders affecting attention and executive control, such as attention

deficit and obsessive–compulsive disorders, schizophrenia, depression and anxiety, are characterized by impaired WM (Egan et al., 2001; Klingberg, Forssberg, & Westerberg, 2002; Purcell, Maruff, Kyrios, & Pantelis, 1998).

Since WM relies on a complex network including subcortical structures (e.g., visual-association areas), frontal and parietal cortical regions, many other neurodegenerative diseases such as Alzheimer's, Parkinson's, Huntington's disease and Lewy bodies dementia can impair WM (Budson & Price, 2005). The PFC is the area mostly involved in WM tasks (Budson & Price, 2005), in which delay-period activity temporarily maintains information (Funahashi, 2017). A growing literature propose the avian NCL as a functional equivalent of the PFC (Lengersdorf et al., 2015). Supporting this view, we indicated in chapter 2, the vINCL as the brain area activated during the WM performance. The vINCL efficiently processed the stimuli information in WM, in pre- and no-cue trials, while inhibiting the irrelevant information. The WM representations were maintained during the encoding and the delays, and modulated by control mechanisms that involved attention, finalized for the task-goal. These phenomenon are highly comparable with the similar abilities involved in the WM network of PFC (Alvarez & Emory, 2006; Funahashi, 2017; Miyake et al., 2000; Stuss & Alexander, 2000). For this reason, the corvid vINCL may contribute significantly to our understanding of prefrontal functions and the neural mechanisms over WM.

2.1. Working Memory and Attention

Humans' success in performing complex tasks depends critically on the ability to selectively process information from the environment (attention) and to retain information in an accessible state over time (WM) (Fougnie, 2008). In WM tasks, cueing an item before stimulus onset (pre-cue) improves the performance (Souza & Oberauer, 2016). Here, we show in crows a similar improvement (chapter 1 and 2). Pre-cue conditions, compared to the no-cue conditions, dramatically maximize the performance, abolishing the load effect. The crows, alike humans and monkeys (Carasco, 2011; Castiello & Umiltà, 1990; Cook & Maunsell, 2002; Maunsell & Cook, 2002; Posner, 1980) easily used pre-cues to facilitate WM during the task. The pre-allocation of attention to the relevant stimulus' location reliably helps the encoding of the sample-array, and through the maintenance, consequently, helps the recall of the sample-array.

Lesions and humans brain imaging studies have identified a distributed network in frontal and parietal cortex that appears to be involved in the allocation of attention (Duncan, 1986; Knight, 1984; Passingham, 1993; Shallice & Burgess, 1991). This includes the FEF, supplementary eye field, anterior cingulate cortex, middle frontal gyrus, intraparietal sulcus, and superior parietal lobe (Corbetta & Shulman, 2002; Hopfinger, Buonocore, & Mangun, 2000; Rossi, Pessoa, Desimone, & Ungerleider, 2009; Ungerleider & G, 2000). Neurophysiology studies in subregions of PFC support patterns of neuronal activity related to attentional state (Schall, 2002) and WM (Goldman-Rakic, 2011; Miller et al., 1996; Quintana, Yajeya, & Fuster, 1988). Those findings suggest that PFC neurons modulate responses in sensory areas during performance of memory and attention tasks (Funahashi, 2017; Miller & Cohen, 2001). The PFC exerts top-down control of attention by means of descending feedback signals, that bias the sensory processing, in favor of behaviorally relevant information (Rossi, Pessoa, Desimone, & Ungerleider, 2009). Thus, selective attention on pre-cue items activates a spatial WM signal specifying a location that should be monitored for the occurrence of a target.

In a similar way, attention acts in the avian functional equivalent of PFC, the vINCL. Selective attention seems to modulate vINCL neurons during WM encoding, like to prioritize stimulus information in the service of WM. In this way, in vINCL the representations of relevant color feature of interest are enhanced in favor of the cued location. However, the encoding is not the end point of selective attention (Gazzaley, 2011): we analysed the effects of attentional cue on color information during the maintenance and the retrieval. Selective attention gathers relevant information and guides a robust maintenance of the information within WM, compared to when the attention is spread over several stimuli until the comparison period, the retrieval. At this stage, the stimuli information in correct trials is not affected by a pre-allocation of attention. Instead, in the same task period, a parallel attentional mechanism provided a much higher encoding to the new test-stimuli to compare for the change detection. As described by McNab et al. (2008), a greater activity in the PFC during the pre-encoding expectation period establishes a filter that prepares and focuses encoding resources. Thus, selective attention not only enables crows to gather relevant information, but it also guides their goal (Carrasco, 2011) maintaining the spatial representation within WM, in order to prioritize the encoding of the novel stimuli to be compared. The presence of attentional mechanisms involved in WM contents in all the stages of information processing are confirmed by a low resolution of color information for irrelevant locations in all the memory stages.

In this case, selective attention suppresses the WM contents for those stimuli that are not relevant for the task goal, in order to optimize the relevant ones (Vogel et al, 2005; Zanto and Gazzaley, 2009). In line with previous studies in prefrontal and parietal subregions, when the focus of attention is distributed over many locations of the visual field, rather than in one, there is a corresponding loss in spatial resolution and processing efficiency for any given location maintained (Buschman et al., 2011; Shintaro Funahashi, 2017; Keitel et al., 2013; Moran & Desimone, 1985). This is in accordance with several theories of attention suggesting that sensory representations compete for neural resources (Bundesen, 1990; Claus Bundesen, Habekost, & Kyllingsbaek, 2005; Desimone & Duncan, 1995; Grossberg, 1980; Rossi et al., 2009). The spatial information of the cue in vINCL neurons during the pre-encoding phase of the stimulus and comparison-array could represent the control mechanism that selectively orient attention to a specific location, a mechanism that usually involve prefrontal and parietal subregion (Bressler et al., 2008; Maurizio Corbetta & Shulman, 2002; Kastner et al., 1999). In line with the mammalian networks involved in attention, the vINCL acts as a multisensory integrative area. It is involved in attentional mechanisms that operate upon perceptual and WM representations, optimizing the use of the limited capacity storage by enhancing the color information from relevant locations, while diminishing the color representations of less relevant locations (Carrasco, 2011). Overall, those empirical findings in the avian model contribute to the literature describing attention as an active modulator involved in the perceptual computations, acting at different levels of information processing (Carrasco, 2011; Nanay, 2015; Reynolds & Chelazzi, 2004).

2.2. Working Memory and Executive control

WM tasks in animals (Dudchenko, 2004) and humans (Miyake et al., 2000) necessarily employ attentional shifting, updating, or inhibitory control on the maintained information (Mochizuki & Funahashi, 2016). To control these different actions in order to achieve the task goal, WM uses the executive control (Perner & Lang, 1999). This is responsible for both the attentive resources and the manipulation of information (Funahashi, 2001). The executive control shifts, updates and inhibits information in WM (Dempster & Corkill, 1999; Miyake et al., 2000; Morris & Jones, 1990; Shilling et al., 2002; Smith & Jonides, 1997).

The shifting attention within WM information engaged by retro-cues is a type of executive control (Berryhill et al., 2012; Brady & Hampton, 2018) that I described in chapter 1. Here, the existence of a retro-cue effect is demonstrated for the first time in crows. Crows possess control mechanisms capable to restrain their attention and manage the accessibility of the relevant information held in WM. The effect mitigated their WM capacity. Crows could use retro-cued locations to increase the quality and quantity of information available to reach the goal-directed behavior (Brady & Hampton, 2018). The behavioral benefits are consistent with the conspicuous human literature on the retro-cue effect (Griffin & Nobre, 2003; Kuo et al., 2012; Kuo, Yeh, Chen, & D'Esposito, 2011; Landman et al., 2003; Nobre et al., 2008; Pertzov et al., 2013; Rerko et al., 2014). Crows outperformed monkeys' retro-cue effect seen in a previous study by Hampton et al. (2018). Monkeys showed a cueing effect constrained to a WM load of 2-colors; when the load increased to 3-colors the monkey did not benefit from retro-cue locations.

Birds have already proved different types of executive functions during laboratory tests (Rose & Colombo, 2005; Veit & Nieder, 2013), although under motivational differences from unequal rewards on remember and forget trials and not tested to control WM-maintenance under the load effect.

It is indeed challenging to test the executive control contribution in WM tasks due to its multifunctional support role. To test the different executive control actions on WM, in chapter 3 we created a WM paradigm including maintenance of the focus of attention, set shifting, updating WM, and inhibition of irrelevant information (Baddeley, 1986; Cowan, 1999; Engle, 2002; Logie, 2011; McCabe et al., 2010; Miyake et al., 2000). In the DMTL task, crows selected and stabilized contingent spatial and remembered cues associations over time, through their selective attention and WM respectively. They suppressed sensory inputs, revealing cognitive inhibition on the irrelevant cues to succeed in the task. Crows efficiently forgot a spatial cue in order to free resources for an active maintenance in favor of the other: a proof of executive control like cognitive flexibility, the ability to quickly and flexibly adapt to changed circumstances (Moore & Malinowski, 2009). Moreover, crows worked efficiently at their maximum memory load while flexible storing, forgetting and updating of multiple task information. An insightful dynamic control of those actions are rule out by the final goal to facilitate the comparison of the spatial cues. The efficient executive control of the memory trace in the transfer, inhibition and update of the rewards information resulted by the dis-

crimination between the differential rewards. The reward magnitudes had an impact on their performance. As seen in humans, corvid's memory is modulated by the reward outcomes associated with color stimuli (Infanti et al., 2015), revealing a distance effect on reward magnitudes previously unseen. Since the difficulties in this novel paradigm could be considered on pair to those found in dual-task and task-switching situations, commonly used in monkeys and humans (Amichetti et al., 2013; Mansouri, Egner, & Buckley, 2017; Stoet & Snyder, 2009; Andreadis & Quinlan, 2010; Dobrynina et al., 2018; Friedman et al., 2008; Liefoghe, Barrouillet, Vandierendonck, & Camos, 2008; Miyake et al., 2000; Strobach, Wendt, & Janczyk, 2018; Vandierendonck, 2014), we propose the DMTL task as an alternative version to test executive control in animal models.

3. The Relationship between Working Memory, Attention and Executive control: is it a common attention construct?

My thesis reveals that crows possess mechanisms of attention and executive control over WM. Those cognitive mechanisms are indispensable aspects of their advanced cognitive abilities. The selective attention abilities seen in these tasks refer to the processing involved in orienting attention towards specific representations while ignoring others. Differently from attentional capture or visual search tasks, in which selective attention operates without any executive demands, the present tasks include executive control mechanisms that could directly refer to the type of attention involved in actions control, related to responding and task execution. In fact, the commonality in both change detection and DMTL tasks, is that selective attention calls on WM through executive control. Specifically, the task necessarily maintains a means-end representation in WM; this representation includes attention selectivity as a means to achieve the task goal, so that the task will tap on executive demands (Vandierendonck, 2014). It has been suggested that depending on the characteristics of the task being executed, selective attention operates with or without executive demands (Vandierendonck, 2014).

Congruent with this idea, the data described in the thesis, proposed a direct role of attention into control mechanisms: attention with its multi-faced construct becomes the biggest support in WM tasks. In our findings attention manages perceptual computations at different levels of the information processing (Macpherson, 2015; Nanay, 2015; Noudoost, Chang, Steinmetz, & Moore,

2010; John H. Reynolds & Chelazzi, 2004). Selective attention acts on WM through, alerting, orienting: whenever the attention is oriented to a relevant location, the location information becomes active and is maintained into this state in WM (Mayr & Kliegl, 2000). Due to these mechanisms, selective attention results in an enhancement of the color information for that location during the entire task period, even in the absence of visual stimuli. The actions are in the perceptual domain (Carrasco, 2011; Egeth & Yantis, 1997; Serences & Yantis, 2006) and in the realm of internal information (Souza & Oberauer, 2016). Attention acts as the executive component required to resolve interference and keep task goals on a volitional basis (Colombo & Cheatham, 2006; Fisher & Kloos, 2016; Kane, Conway, Hambrick, & Engle, 2007; Miller et al., 2018; Posner & DiGirolamo, 1998; Posner & Petersen, 1990; Posner & Rothbart, 2007).

Selective attention exerts a top-down control over which items will occupy the limited WM storage and thus prioritizing the information processing of the most relevant items for the current processing goals in a form of executive attention (Ku, 2018). In line with this characteristic, attention facilitates the encoding of the stimuli to be compared in the most critical part of the change detection task, enhancing the stimulus information on attentive locations during the decision-making process. It actively controls the relevant information for the task goals, while suppressing the irrelevant ones during the entire task period as inhibitory function.

The same peculiarity of executive attention may be involved in the retro-cue effect. As pre-cued items, attention can induce a robust encoding of the retro-cued locations in WM during the retention interval. The retro-cued locations are now protected from time-decay and from perceptual interference (Souza & Oberauer, 2017) and they can influence the comparison: the encoding of the new WM contents is prioritized, similar to pre-cue information.

The execution of those tasks requires relevant representations to remain active until the task is completed, because active is the attentional control over the task goals. Loss of executive attention results in loss of memory contents, as an erroneous change detection or as consequence of volitional control. In fact, we speculate that in the small reward pairs of the DMTL task, considered irrelevant information from the crows, the selective attention is not bind with an executive control, such that triggers only suppressor mechanisms on the information. This could directly add a volitional nature of the control mechanism on selective attention.

The hypothesis that attention shifts, updates and inhibits information is in accordance with the supervisory attention model of Norman and Shallice (1986), in which attention plays the role of

the central executive to control actions (Vandierendonck, 2014). The conceptualization of the term executive attention is not new. It is similar to that of Engle, Kane, and colleagues (Engle & Kane, 2004; Engle et al., 1999; Kane et al., 2007) where the main functions of the executive attention are the ability to maintain a goal in an active state during task performance (Banich, 2009; Braver, Gray, & Burgess, 2007; Desimone & Duncan, 1995; Mangun, 2012) and the ability to resolve interference (Braver et al., 2007; Norman and Shallice, 1986; Persson & Reuter-Lorenz, 2008). The ability to control attention during goal-directed activities, seen in those tasks, can unify executive and selective attention and point-out their essential symbiosis in being triggered, whenever necessary, to generate an efficient WM system (Friedman et al., 2008; Miyake et al., 2000).

4. Future studies

The present WM paradigms under control setups, can yield to a variety of future directions to bring into animal models and human experiments. Previous behavioral and neurophysiological studies in crows did not allow the dissociation of the cue-effect and executive mechanisms over WM, under challenging memory loads (see chapter 1, 2 and 3). Due to their versatility, these paradigms can be adapted to perform comparative studies on attention and executive control.

We find that vLNCL neurons, actively modulated by WM contents, is a target area of attentional modulation. The area should be tested in many other domains of attentional selection: i.e. feature-based within the dimension of motion or object-based. Electrophysiological studies in vLNCL could display the bidirectional action of selective attention on WM from the pre- to the retro-cue conditions. Moreover, introducing distractors, we could test inhibitory mechanisms of attention in vLNCL. Moreover, in order to elucidate the retrieval of the color information during the comparison period, we performed single-cell recordings on the corvid vLNCL during a similar version of the present task. In the experiment, we compared a single-probe to a whole display recognition: the current analysis will allow to address the influence of the load effect during the retrieval of the color information.

Further investigations could open-up to a general constraint of the neural processing, involved in the control and effects of attention in WM from the avian pallial nuclei to the mammalian

cortex. Thus, we believe that extensive research needs to focus on the different nuclei or neural mechanisms in the avian brain.

We targeted, for the first time, the recently identified mNCL, (see chapter 2) characterized by high density of DA neurons (von Eugen, 2017; Sen et al., 2019). Importantly, the neural modulation of different task parameters had no impact on the WM contents of this task. The divergent findings reported in chapter 2 need to be supported with electrophysiological recordings from other paradigms, that involve attention orientation in the auditory domain, due to its anatomical proximity with NCM. Furthermore, anatomical studies are necessary in order to convey the precise position of the targeted area. The carrion crow atlas could significantly help in the definition of visual areas usually involved in the focus of attention (e.g. archipallial gaze field, the optic tectum with midbrain components) (Sridharan et al., 2014).

Future electrophysiological recordings in crows vNCL could reveal the neuronal implementation of the complex cognitive processes in birds reported in chapter 3. The DMTL task represents a controlled behavioral paradigm for executive control, adaptable to comparative studies that can be used for electrophysiological examinations. Single-cell activity recordings in vNCL and visual areas (e.g., wulst, entopallium) has the potential to enlighten how the neural substrates integrate different task information, between maintenance and forgetting or updating of information, until the decision is made.

In addition, detecting neural oscillations in the avian brain could show specific patterns of interplay activity in WM between different wave frequencies: e.g. during correct and incorrect responses, as previously observed in monkeys (Miller et al., 2018). A local field potential (LFP) analysis is ongoing in the change detection task reported in chapter 2. Indeed, having recorded the low frequencies from multiple NCL sites, we could find increased gamma-frequency synchronization of NCL neurons representing the relevant stimulus, as previously shown in monkeys in visual and prefrontal neurons (Fries, Reynolds, Rorie, & Desimone, 2001; Lundqvist et al., 2016). Few labs have investigated neural oscillations in the avian brain (Goddard, Sridharan, Huguenard, & Knudsen, 2012; Goddard, Sridharan, Huguenard, & Knudsen, 2012): if they are a general means of information processing, very similar patterns of activity should be tested in the change detection task to observed in the corvids brain as in the primates brain a communication between different brain areas (Pinotsis, Buschman, & Miller, 2019). Furthermore, our technical achievements in building touch screen-equipped operant-chambers with custom-made automatic feeder, and a head-tracking system

of two high-speed cameras are the control setups suitable for combined behavior, electrophysiology and optogenetics experiments in animal research. A third camera to the head-tracking system could additionally allow to have the eye tracking in unrestrained birds, which could reveal mechanisms of covert and overt attention in the WM task (Kulke, Atkinson, & Braddick, 2016).

5. Conclusion

WM has been extensively investigated in humans, in an interdisciplinary way, with thousands of articles and books published on the topic. Its central role in human life highlights its evolutionary and historical relevance (Carruthers, 2013), which can be further elaborated in animal models. This research displays the translation of convergent evolution patterns on behavioral and neuronal basis of complex WM capabilities in crows, a species evolved independently from mammals more than 300 million years ago. The assumption that a bird like a crow possesses cognitive control in memory resources may help to explain their exquisite behavior and understand the neural basis of cognition.

Concluding, we showed that the cognitive capacity of corvids is ruled out by attentional and executive control, like for humans, and the principal area of interest under the visual domain is the vNCL, compared to the mNCL. The vNCL, like higher-order cortical areas, utilizes attention to modulate the WM processing, by reinforcing the relevant information so that the task goals could be achieved. This opens up to a general constraint of neural processing where WM through selective attention and control mechanism monitor its resources and improve performance. The fact that this powerful WM system exists without a layered cerebral cortex, means that evolution in birds and in mammals solved independently. The striking nuclei-organization of corvid brain offers an important proof that cognitive abilities do not linearly scale with evolutionary distance from humans, and that crow research offers an important distinctive view on the brain.

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Dedicated to my grandma Gemma,
because you forgot my name but not how much I love you.

CURRICULUM VITAE

Erica Fongaro

Work Experience	PhD Candidate	Jan. 2017
	• Ruhr-Universität Bochum (RUB)	May 2019
	<i>Avian Cognitive Neuroscience (Dr. Jonas Rose)</i>	
	• Universität Tübingen	Apr. 2015
	<i>Animal Physiology (Dr. Jonas Rose)</i>	Dic. 2016
	Research Internship (Master's Thesis)	Mar. 2013
University of Trieste (Italy)	Dic. 2013	
	<i>Center for Studies in Behavioral Neurobiology</i>	
	<i>(Prof. Cinzia Chiandetti)</i>	
	"The role of different bridging stimuli in dogs' learning abilities".	
	Research Internship (Bachelor's Thesis)	
	University of Ferrara (Italy)	
	<i>Biochemistry and Clinical Biochemistry</i>	Jan. 2011
	<i>(Prof. Franco Dallochio)</i>	Dic. 2011
	"Study of dimer/tetramer equilibrium in Trypanosoma brucei 6-phosphogluconate dehydrogenase".	
Education	Diploma in Neurosciences (M.Sc)	Jan. 2012
	University of Trieste (Italy)	Mar. 2014
	<i>In collaboration with the</i> <i>Scuola Internazionale Superiore di Studi Avanzati (SISSA) di Trieste</i>	

Diploma in Molecular Biology (B.Sc)

University of Ferrara (Italy)

Department of Life Sciences (Biology)

Skills

Research skills:

Surgeries (Chronic Electrophysiological implants & stereotaxic)

Anaesthesia in Birds: Monitoring, Injections / blood sampling

In vivo electrophysiological recordings and analysis,

Cognitive tests, Operant conditioning, Clicker training

Behavioral scoring/tracking software

PCR, qPCR, DNA/RNA/protein extraction, Western blot,

cell-culture maintenance, cell transfection and electroporation,

gel electrophoresis of RNA and DNA samples,

in vitro transcription, in vitro translation,

Dynamic Light Scattering (DLS) and

isothermal titration microcalorimetry (ITC).

Computer skills:

Matlab, SPSS,

Excel, Visual basics (VBS)

Languages:

Italian (native), English (C1)

German (A2), French (A2)

Scientific

Papers

Selected Journal Articles:

C. Chiandetti, S. Avella, **E. Fongaro**, F. Cerri (2016)

“Can clicker training facilitate conditioning in dogs?”.

Selected

Meetings

Conference Papers / Poster / Talks:

Talk at Avian Cognitive Neuroscience 2018 (ACN 2018)

Corvids display attentional control over visual working memory.

FENS forum of neuroscience, *Posters presentation*

1. 2016: **E. Fongaro**, L. Hahn, J. Rose

2. 2018: **E. Fongaro**, D. Balakhonov, J. Rose

