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Multimodal information processing in the domestic chick (*Gallus gallus*): role of precocial cognitive abilities and predispositions

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With love and gratitude to all the animals.

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ABSTRACT

A crucial ability for animals' survival is to quickly process and respond to novel situations. Yet, the amount and variety of sensory input coming from the environment greatly exceeds the brain's processing capacity. To overcome this limit, animals can implement several mechanisms to select and prioritize relevant information. Whereas some of these mechanisms require a considerable effort, both in terms of physical and cognitive resources, others rely on cognitive predispositions, attentional biases, or hemispheric specializations, and can be spontaneously employed by the animals with little or no costs. This work focuses on the precocial mechanisms that favour an initial positive interplay with the environment. The selected model species, the domestic chicken (*Gallus gallus*) might be considered optimal, or at least the most convenient, to this aim, as being precocial species, young chicks must be able to interact autonomously with the environment immediately after hatching, thus making it possible for us to study the very early stages of cognition and spontaneous information-processing mechanisms. Section 1 focuses on spontaneous multimodal information integration. In particular, three cases of multimodal information integration are investigated: the spontaneous acquisition of a visuospatial conditioned rule in long-term memory (Study 1), the predisposition to match non-redundant multimodal information with respect to the case of visuospatial crossmodal correspondences (Study 2), and the facilitation effect resulting from a spontaneous precocial association between spatial and numerical information (Study 3). Section 2 focuses on processing modality selection and strategies. A crucial ability to ensure a successful interaction with the environment is that of selecting the optimal processing modality and cognitive strategy among a repertoire of possible alternatives. Study 4 provides evidence of a non-mathematical mechanism based on perceptual grouping on which 1-day-old chicks can rely to solve complex numerical discrimination. Study 5 further deepens the emergence and

functioning of such a mechanism, showing that chicks are capable of selecting a perceptual-based or a magnitude-based mechanism depending on a joint analysis of their internal goals and environmental settings. Overall, chicks proved capable of extracting multimodal and unimodal information in several unsupervised (i.e., in the absence of any formal training or experience) situations and of relying on the corresponding mental representations to solve different tasks successfully.

ABSTRACT (Italian version)

Un'abilità cruciale per assicurare ad un organismo la sopravvivenza è essere in grado di processare e rispondere velocemente a nuove situazioni. Tuttavia, la quantità e la varietà di input sensoriali che arrivano dall'ambiente esterno eccedono notevolmente le capacità di processamento del cervello. Per poter far fronte a tale limite, gli animali possono implementare diversi meccanismi atti a selezionare le sole informazioni rilevanti. Nonostante alcuni di questi meccanismi siano vincolati da una notevole richiesta energetica, sia in termini fisici che cognitivi, vi sono altri meccanismi che si basano su predisposizioni cognitive, *bias* attentivi e specializzazioni emisferiche. Questi possono essere messi in atto spontaneamente dagli animali e richiedono un minimo, se non nullo, costo energetico. Il presente lavoro è dedicato allo studio dei meccanismi precoci che vengono utilizzati dagli animali per garantire un primo scambio positivo con l'ambiente. Il modello di ricercar selezionato, ovvero il pulcino di pollo domestico (*Gallus gallus*) risulta ottimale per questo scopo. Infatti, essendo una specie precoce, il pulcino deve essere in grado di interagire autonomamente con l'ambiente già dai primi istanti dopo la schiusa, rendendo quindi possibile lo studio delle capacità cognitive precoci e delle predisposizioni innate nel processamento delle informazioni. La Sezione 1 è dedicata alla integrazione spontanea delle informazioni multimodali. In particolare, vengono analizzati tre casi di integrazione delle informazioni provenienti da diverse modalità sensoriali: l'acquisizione spontanea di regole condizionali in memorial a lungo termine (Studio 1), la predisposizione a elaborare congiuntamente informazioni non ridondanti, con particolare riferimento al caso delle corrispondenze crossmodali visuospaziali (Studio 2) e l'effetto di facilitazione risultante dal possedere un codice di rappresentazione innato che associa informazioni spaziali e numeriche. La Sezione 2 è dedicata allo studio della selezione della modalità di processamento e delle conseguenti strategie cognitive attutate dall'animale. Infatti,

è fondamentale, per garantire il successo nell'interazione con l'ambiente esterno, saper selezionare la modalità di processamento ottimale all'interno di un repertorio di possibili alternative. Lo Studio 4 analizza un caso di meccanismo di processamento percettivo basato sul raggruppamento che permette a pulcini di un giorno di vita di risolvere complesse discriminazioni numeriche. Lo Studio 5 approfondisce lo sviluppo e il funzionamento di tale meccanismo, mostrando come i pulcini siano in grado di selezionare un meccanismo basato sull'analisi percettiva o della grandezza numerica, in base ad un'analisi congiunta dei loro obiettivi interni e delle richieste ambientali. In conclusione, questo lavoro mostra come i piccoli di pollo domestico siano in grado di estrapolare informazioni multimodali e unimodali in diverse situazioni sperimentali in cui non vi è alcun addestramento formale (dunque in maniera spontanea ed automatica). Si è visto inoltre come i pulcini siano in grado di processare mentalmente tali informazioni (in maniera congiunta o unimodale) e di utilizzare la corrispondente rappresentazione mentale per rispondere adeguatamente alle diverse richieste dell'ambiente.

SUMMARY

In a world that continues to evolve and change, it is crucial for animals' survival to quickly process and respond to novel situations. Yet, the amount and variety of sensory input coming from the environment greatly exceeds the brain's processing capacity. To overcome this limit, animals can implement several mechanisms to select and prioritize relevant information. This could be done by extrapolating regularities and learning co-occurrences[1–3], remembering previous experiences[4,5] and recognizing novelty[6,7], or creating expectancies and reasoning in terms of outcome probabilities[8–11]. All these mechanisms, however, require some cognitive effort and are not always immediate (i.e., they might need time for processing the information and planning the response), thus they do not appear optimal when facing rapid environmental changes. Hence, to increase their chances of survival, animals might benefit from faster, low-cognitive-demanding mechanisms for the immediate processing of perceptual and sensory information. These mechanisms include behavioural and cognitive predispositions, attentional biases, or hemispheric specializations. In fact, humans and other animals might be endowed with some specialized systems and mechanisms that favour an initial positive interplay with the environment and onto which new flexible skills and knowledge could be further built as a result of experience[12–14].

The present work aims to investigate the role of predispositions and early-available mechanisms on processing information from different sensory modalities in an avian model, the domestic chicken (*Gallus gallus*). In particular, in all the studies broiler Ross 308 chicks were used. Chickens have been proven to possess extremely sophisticated behaviours and cognitive abilities, comparable to not only other avian species but also humans and other mammals[15–19]. Moreover, as a precocial species, young chicks must be able to interact autonomously with the

environment immediately after hatching, thus making it possible for us to study the very early stages of cognition and spontaneous information-processing mechanisms[15,20].

Section 1 focuses on spontaneous multimodal information integration.

In some cases, stimuli coming from the environment might relate to each other in a conditional manner. For instance, a certain visual cue is predictive of the presence of food only when occurring with a certain auditory cue, whereas each individual cue per se is not sufficient. **Study 1** explores whether young chicks are sensitive to such a correlation of multimodal cues. It tests whether 5-day-old chicks can spontaneously create an already integrated mental representation of a visuospatial conditioned rule in long-term memory.

In some other cases, animals are not required to create de novo integrated representations; instead, they can rely on inborn predispositions to match objects' specific physical properties. This is the case of crossmodal correspondences, a phenomenon for which we tend to associate non-redundant information spontaneously in the absence of any explicit rule[21,22]. For instance, we tend to match bright stimuli with high-pitch sounds and dark stimuli with low-pitch sounds[22], or we consider lemon scent as "more spiky" and vanilla scent as "more rounded"[23]. Crossmodal correspondences were vastly reported in mammalian species[22,24–26], suggesting a shared origin of this mechanism in our clade. In addition, the fact that crossmodal correspondences were reported in preverbal infants[27,28] indicates that they require little or no dedicated experience. Yet, no conclusive evidence is available on this because, in our own species, it would be impossible to eliminate completely the role played by fast post-natal learning[29]. **Study 2** provides the first evidence of a case of crossmodal correspondences (i.e., space–luminance association) in 3-day-old chicks, which aims to address the origin of such a phenomenon from ontogenetic (i.e., by controlling post-hatching experience) and phylogenetic (i.e., by testing a non-mammalian species) perspectives.

Interestingly, baby chicks are already known to be susceptible to a peculiar case of cross-domain interaction, even though it does not completely satisfy the definition of crossmodal correspondence (i.e., it is not directly linked to objects' physical properties). This is the case of the predisposed association between spatial and numerical information (SNA) for which chicks (and other species, including humans[30–33]) possess a left-to-right oriented representation of numerical magnitude[34,35]. Even though SNA is widely attested in young chicks, it is still unknown in what measure such a predisposition to map magnitude onto space could affect early perceptual and attentional mechanisms. To answer this question, **Study 3** investigates whether congruency between spatial and magnitude information could support a complex discrimination that chicks otherwise fail, i.e., the three versus four comparison. This allows for role clarification of task complexity and cognitive resources on SNA and explores whether this inborn mental representation could act as a cognitive support in numerical tasks by stressing a redundancy in multimodal information.

Section 2 focuses on processing modality selection and strategies. A crucial ability to ensure a successful interaction with the environment is that of selecting the optimal processing modality and cognitive strategy among a repertoire of possible alternatives. In fact, there are cases in which the information coming from the different sensory domains could conflict or prompt different strategies (hence different results). It is crucial for animals, when facing a complex stimulus or situation, that they are capable of selecting the one that most probably leads to the desired outcome.

Study 4 provides evidence of a non-mathematical mechanism based on perceptual grouping on which 1-day-old chicks can rely to solve complex numerical discrimination. Chicks seem to represent and mentally manipulate sets of elements by disassembling them into smaller subgroups, creating, when possible, all equal-sized subgroups. Eventually, birds could rely on such a perceptual symmetry to discriminate against sets for which it is not possible to create equal-sized subgroups (i.e., groups with prime numerosities). As chicks were previously habituated to sets of all even numerosities (i.e., all allowing for symmetrical grouping), the preference for sets without asymmetrical configurations was interpreted as a response to the novelty of such stimuli.

A perceptual grouping strategy could enable chicks to solve complex discrimination at which they otherwise would be likely to fail (i.e., if employing a numerical-based processing). Interestingly, such a mechanism appears to be spontaneously carried out by newly hatched chicks, and it is based on their predisposition for symmetrical patterns[36] and novelty exploration[37,38].

However, although this peculiar perceptual strategy could enable chicks to solve complex discrimination, its ecological value for the animal is strictly related to the task requirements, i.e., seek the stimulus that mostly differed from those to which chicks were previously habituated. The same strategy would be ineffective in a different scenario, for instance in a social context in which the chick is looking for its rearing companions. In this latter case, the optimal answer would be that of locating the largest group of familiar individuals[19,39,40] (thus a numerical strategy) rather than novelty detection. It is yet to be determined whether numerical-based and perceptual-based mechanisms are equally available at the early stages of life and could be flexibly selected by the chicks to answer different environmental requests. **Study 5** aims at answering this question by testing two groups of chicks in the same numerical comparison (i.e., 5 vs 9) by stressing either the testing stimuli novelty (the novel stimulus being the smaller in the comparison) or the social component of the stimuli (thus prompting a preference for the larger set). The fact that chicks could show a task-based response, modifying their behaviour according to the two different environmental requests, could be considered as evidence of their capability to address their own behaviour based on a joint analysis of their previous experience, internal motivation, and perceptual analysis of the context.

SUMMARY (Italian version)

In un mondo in continua evoluzione e mutamento, saper processare velocemente le nuove informazioni, e rispondere prontamente ai cambiamenti dell'ambiente, risulta fondamentale per la sopravvivenza. Tuttavia, la quantità e la varietà di stimolazioni sensoriali provenienti dall'ambiente eccedono di gran lunga le capacità di processamento del cervello. Dunque, per far fronte a tale limite, gli animali possono implementare una serie di meccanismi atti a selezionare, all'interno della pletora di informazioni esterne, quelle necessarie a risolvere di volta in volta diversi compiti (ad esempio rilevare la presenza di un predatore, di una preda, trovare i propri compagni sociali, etc.).

Per fare ciò, gli animali possono fare affidamento a diverse strategie, come estrapolare regolarità ed apprendere pattern di co-occorrenza[1–3], ricordare esperienze precedenti[4,5] e riconoscere situazioni/stimoli nuovi[6,7] o creare aspettative e ragionare in termini probabilistici[8–11]. Tuttavia, tutti questi meccanismi richiedono un certo sforzo cognitivo per essere messi in atto e non sempre sono immediati (i.e., è possibile che sia necessario del tempo per processare le informazioni e pianificare una risposta adeguata), per cui potrebbero non essere ottimali per rispondere a cambiamenti ambientali repentini e/o inattesi. Al fine di incrementare le loro *chance* di sopravvivenza, gli animali devono quindi basarsi su sistemi di processamento con un basso dispendio di risorse cognitive che possano garantire una prima rapida analisi delle informazioni percettive e/o sensoriali in ingresso. Questi sistemi di processamento sono rappresentati da predisposizioni cognitive, *bias* attenzionali e specializzazioni emisferiche. Infatti, è possibile supporre che gli animali (incluso l'essere umano) siano dotati di sistemi specializzati e meccanismi atti a favorire un iniziale scambio positivo con l'ambiente circostante. Su tali meccanismi si andranno poi a costituire nuove abilità e conoscenze come risultato delle esperienze dell'individuo[12–14].

Lo scopo di questo lavoro è studiare il ruolo delle predisposizioni e dei meccanismi di processamento delle informazioni disponibili già dai primi istanti di vita in un modello aviario, i.e., il pulcino di pollo domestico (*Gallus gallus*). Nello specifico in tutti i lavori presentati di seguito sono stati utilizzati pulcini di razza broiler Ross 308. Il pollo domestico è stato ampiamente studiato per le sue capacità cognitive, che possono essere considerate al pari di altri uccelli ed anche dell'essere umano e di altri mammiferi[15–19]. Inoltre, trattandosi di una specie precoce, i pulcini di pollo domestico devono essere in grado di interagire autonomamente con l'ambiente già dai primi istanti di vita dopo la schiusa dell'uovo. Questo li rende un modello eccellente per lo studio delle abilità cognitive e dei meccanismi precoci di processamento delle informazioni[15,20].

La **Sezione 1** è focalizzata sullo studio delle capacità spontanee di integrazione delle informazioni provenienti da diverse modalità sensoriali.

In alcuni casi, le stimolazioni ambientali possono essere legate da relazioni condizionali. Ad esempio, un certo indizio visivo può essere indicativo della presenza di cibo, ma solamente quando è presente anche un secondo indizio uditivo. Dunque, ciascun indizio preso singolarmente non è sufficiente, ma, per risolvere il compito (nell'esempio, localizzare correttamente la fonte di cibo) è necessaria la loro compresenza. Lo **Studio 1** è volto ad indagare se i pulcini siano sensibili a queste correlazioni di indizi multimodali. A questo scopo, vengono testati pulcini di 5 giorni di vita, per indagare se questi siano in grado di formare spontaneamente una rappresentazione integrata in memoria a lungo termine di una regola condizionale tra informazione visiva e spaziale.

In altri casi, tuttavia, agli animali non è richiesto di creare rappresentazioni mnestiche *ex-novo*, ma piuttosto di basarsi su predisposizioni innate a legare specifiche proprietà degli oggetti. Questo è il caso delle corrispondenze crossmodali, un fenomeno per cui noi tendiamo ad associare spontaneamente delle caratteristiche fisiche degli oggetti in assenza di una regola che le leghi[21,22]. Ad esempio, noi associamo stimoli ad alta luminosità con suoni acuti e stimoli a bassa luminosità con suoni gravi[22]. In maniera simile, definiamo l'aroma di limone come "più spigoloso" e l'aroma di vaniglia come "più tondo"[23]. Le corrispondenze crossmodali sono state ampiamente attestate nei mammiferi[22,24–26], supportando l'idea di un'origine condivisa di tale meccanismo (per lo meno all'interno di questa classe animale). Inoltre, poiché ci sono esempi di corrispondenze crossmodali anche in infanti preverbali[27,28] è possibile supporre che queste richiedano poca (o addirittura nessuna) esperienza specifica per avvenire. Tuttavia, quest'ultima ipotesi è ancora largamente dibattuta, in quanto nessuno studio è riuscito in maniera convincente a disambiguare il ruolo del rapido apprendimento post-natale degli infanti[29]. Lo **Studio 2** fornisce una prima evidenza di un caso di corrispondenza crossmodale (i.e., l'associazione spazio-luminanza) in pulcini di 3 giorni, cercando di ampliare l'attuale conoscenza di tale fenomeno sia dal punto di vista ontogenetico (i.e., controllando le esperienze post-natali) che filogenetico (i.e., avendo come modello di ricerca un uccello ovvero un membro di una Classe animale differente dai mammiferi).

È interessante notare che in degli studi precedenti è stato già mostrato come i pulcini siano soggetti ad un caso particolare di interazione tra informazioni appartenenti a diversi domini sensoriali. Questo caso non rientra a pieno titolo tra le corrispondenze crossmodali, in quanto non si fa riferimento diretto a proprietà fisiche degli oggetti, ma rappresenta comunque un importante esempio di associazione multimodale. Si tratta della predisposizione riscontrata in pulcini di pochi giorni di vita (ed anche in altri animali adulti, incluso l'essere umano[30,31], e in neonati umani[32,33]) ad associare l'informazione numeriche con una rappresentazione spaziale orientata da sinistra verso destra (*Space Number Association – SNA*)[34,35]. Rimane tuttavia da chiarire in che misura tale predisposizione ad associare spazio e numero possa avere un effetto sui primi meccanismi percettivi ed attentivi di processamento delle informazioni. Per rispondere a tale domanda, lo **Studio 3** analizza se la congruenza tra informazione numerica e spaziale (i.e., quando le numerosità maggiori sono collocate nell'emispazio destro) possa supportare la *performance* di pulcini di 4 giorni di vita in una discriminazione numerica complessa, ovvero il confronto 3*vs*4. In questo modo, è possibile chiarire il ruolo della complessità del compito e della richiesta di risorse cognitive nel determinare l'effetto di *SNA*, nonché approfondire ulteriormente tale processamento multimodale, per comprendere se esso possa agire come supporto cognitivo in un compito numerico complesso.

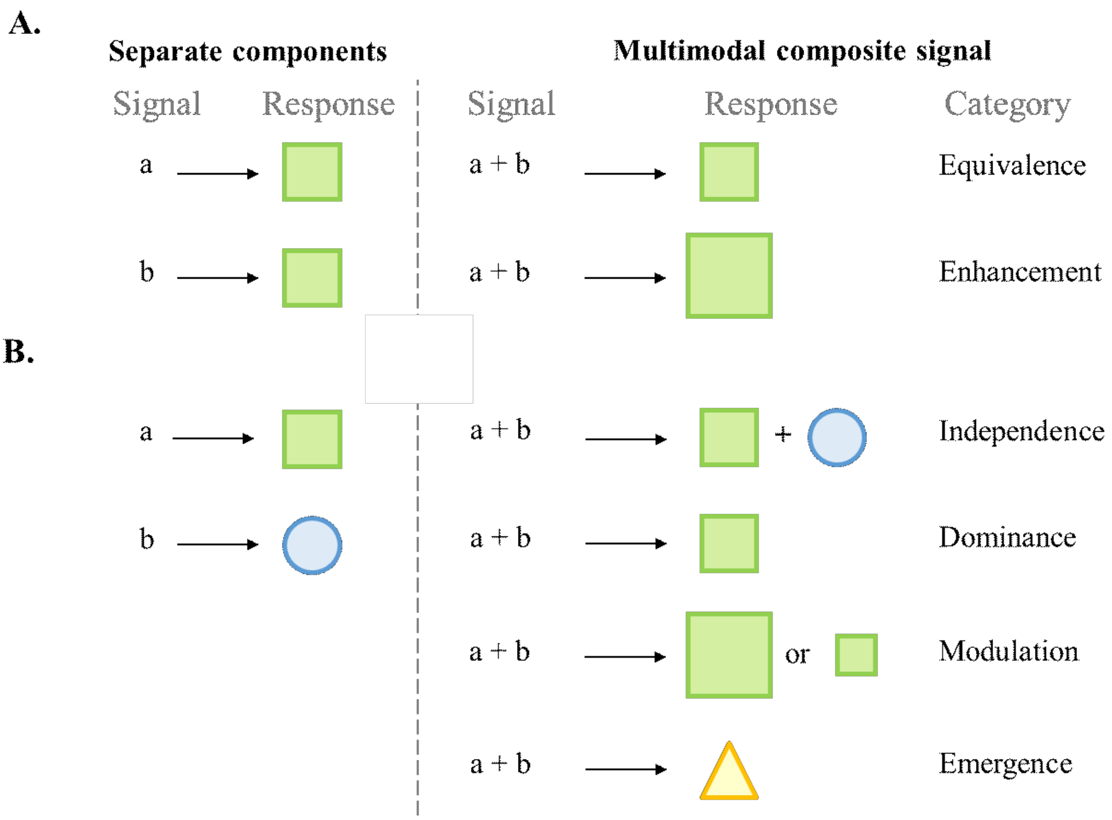
La **Sezione 2**, è focalizzata sui processi di selezione di diverse strategie di processamento tra diverse modalità sensoriali. Risulta infatti di vitale importanza per gli animali, in presenza di diverse fonti di stimolazione sensoriale, saper selezionare la modalità di processamento più appropriata per risolvere il compito e per giungere quindi all'*outcome* desiderato. Questo è particolarmente rilevante se si considerano quelle situazioni in cui vi è un conflitto tra le informazioni provenienti da diverse modalità sensoriali. In questi casi è cruciale per l'animale essere in grado di selezionare, all'interno di una gamma di possibili strategie di processamento, quella che più probabilmente può portare all'esito più favorevole.

Lo **Studio 4** fornisce un'evidenza sperimentale di un meccanismo non-numerico basato sul raggruppamento percettivo, che i pulcini possono adoperare per risolvere compiti complessi di discriminazione numerica. Questo permette loro di distinguere tra due gruppi, anche di elevate numerosità, il set che permette il raggruppamento simmetrico da quello in cui questo tipo di raggruppamento è impossibile (i.e., essendo un numero primo). Poiché i pulcini erano stati abituati prima del test ad una serie di numerosità pari (i.e., che permettono sempre un raggruppamento simmetrico) la preferenza al test per la numerosità per cui era possibile solo creare configurazioni asimmetriche è stata interpretata come una preferenza per il set nuovo. Tale meccanismo di raggruppamento percettivo sembra essere messo in atto spontaneamente dai pulcini, e si basa su una predisposizione innata per i pattern simmetrici[36] e per l'esplorazione di stimoli nuovi[37,38]. È interessante notare che tale strategia percettiva permette ai pulcini di risolvere determinati confronti numerici, anche molto complessi, ma che, essendo basata sull'esplorazione del nuovo/diverso, non sempre si rivela adeguata. Ad esempio, qualora il compito richiesto al pulcino fosse quello di identificare il più grande dei due set (e.g., per ritrovare il maggior numero possibile di compagni sociali) tale strategia si rivelerebbe fallimentare, e andrebbe invece preferita una strategia matematica[19,39,40]. Lo **Studio 5** è atto a indagare se i pulcini neonati siano in grado di selezionare efficacemente due diverse strategie di processamento (i.e., percettivo vs numerico) per risolvere uno stesso compito di discriminazione numerica (i.e., 5vs9) per rispondere a due differenti richieste ambientali (i.e., individuazione del nuovo o del gruppo maggiore, rispettivamente).

SECTION 1 – MULTIMODAL INTEGRATION OF INFORMATION

Animals are continuously exposed to a plethora of stimulations, coming from different sources and sensory modalities. Some of these can provide redundant information (i.e., they convey the same meaning), whereas others can be non-redundant, with each having its individual meaning[41]. Animals need to select the relevant information and create a coherent representation to rely on when interacting with their environment. Partan and Maler (1999) tried to provide an exhaustive theoretical frame for the study of multimodal integration by defining the characteristics of all the possible integration processes and outcomes[41]. The authors distinguished between redundant and non-redundant information. When there is a redundancy (**Fig. 1A**), each stimulation taken alone is still sufficient to convey the (same) message, however the combined presence of multimodal signals could enhance its intensity, leading to an increased accuracy and speed and a decreased perceptual threshold (i.e., animals require less intense stimulations to detect the stimuli)[42,43]. For instance, humans and rhesus monkeys spontaneously create a multimodal representation of familiar individuals in which they match visual (i.e., the face) and auditory (i.e., the voice) information. Eventually, they could successfully rely on either cue for social and individual recognition, although they perform better when both are available[42,44]. Chickens proved able to detect minimal differences between a target and a testing stimulus, with optimal performance when visual (a short flash) and auditory (a beep sound) information were presented together. Baby chicks also showed an increased imprinting reaction to artificial and naturalistic stimuli when these could be processed in a multimodal manner (i.e., they possessed visual and auditory components)[45].

In the case of non-redundant information (**Fig. 1B**), each source conveys a different meaning. In some circumstances, each stimulation guarantees a positive interaction with the environment, with the multimodal integration leading to an enhancement effect similar to that for cases of redundant information. Alternatively, one modality might dominate over the other, resulting in a unimodal representation. Lastly, there are cases in which each source is necessary but insufficient, and they need to be integrated to be effective[46,47]. For example, young chicks do not respond to aposematic coloration (i.e., red and yellow preys) or odour (i.e., pyrazine) when presented individually, whereas they show a strong avoidance reaction when these are presented together[46]. Thus, multimodal stimulation evoked a new behaviour not elicited by the unimodal components. As it is a way to modulate organism–environment interaction, multimodal integration of non-redundant information can be observed in different species that face similar environmental pressures, including some invertebrate models. For instance, black garden ants proved capable of multimodal learning of a spatial conditional rule[47]. To locate food correctly, ants had to remember its position based on an integrated representation of the context (i.e., whether it was a blue or a yellow maze) and the spatial position (i.e., left or right). Each form of information per se was not sufficient to solve the task, and the ants needed to rely on a cohesive memory of both (e.g., go to the left in the blue maze and to the right in the yellow one).



Adapted from: Partan & Marler (1999).

Fig. 1 Theoretical frame for multimodal integration[41]**.** In the example, there are two sources of information (**a** and **b**). **A. Redundancy:** when the sources of information are redundant (i.e., they convey the same meaning) two possible scenarios are to be expected: i. **a** and **b** combined representation leads to the same outcome as for each of them individually (equivalence); ii. the original meaning remains unvaried, but the combined representation is strengthened in intensity (enhancement). **B. Non-redundancy:** when **a** and **b** have different meanings (non-redundancy), one of four possible outcomes is to be expected: i. **a** and **b** are not combined, and each conveys its meaning without interacting with one another (independence); ii. one information prevails and nullifies the other (dominance); iii. one information prevails, but the other still has an effect in modulating (strengthening or weakening) its intensity (modulation); and iv. when **a** and **b** are integrated in a single representation, this conveys a third meaning, different from both **a's** and **b's**.

Study 1 provides evidence of the latter case (emergence) and focuses on the role of long-term memory in storing and retrieving the integrated representation. Studies on long-term memory have not yet reached a consensus on the stored representations' characteristics to clarify at what stage information integration takes place[48]. For the subject to use the knowledge gained from their experience, it is necessary to integrate each property of the experience in a coherent and integrated representation. However, it is still unclear whether there is an initial multimodal integration of information when creating the memory engram (encoding/storing), or whether each piece of information is stored in a dedicated sensory-related system, with the integration process taking place afterwards (retrieval).

Study 2 takes into account a peculiar case of multimodal integration, which was not considered in the original theoretical framework proposed by Partan and Maler (i.e., crossmodal correspondences). These consist of a spontaneous tendency to associate non-redundant information from different sensory modalities in the absence of any explicit rule that matches them[21,22,29]. For instance, in the case of the aforementioned example, garden ants matched the visual (i.e., colour of the maze) and spatial (i.e., left or right arm of the maze) information because this allowed them to locate the food reward correctly (e.g., on the right arm in the blue maze; on the left arm in the yellow one)[47]. If the combined representation of visual and spatial information was not predictive of the food source, ants had no reason to prefer the right blue arm and the left yellow arm, and they would probably have chosen either arm–colour combination at chance level. In the case of crossmodal correspondences, however, in spite of no apparent benefit for the animal to match multisensory information, there is a spontaneous and shared tendency (at least in the mammal clade, which is the only one that has been studied to present[22,24,26,49]) to associate particular physical properties of the objects. For instance, low luminosity is associated with the left hemispace or with low-pitched sounds, and high luminosity is associated with the right hemispace or with high-pitched sounds[22,26,50]. Interestingly, as in the enhancement case seen for redundant information[41,45], the combined presence of multimodal stimulation supports performance (i.e., faster reaction times and higher accuracy) in the case of crossmodal correspondences[21]. However, the origin of such a mechanism is still unclear, and there is an open debate on whether crossmodal correspondences are innate (e.g., they could be the first rapid pathway for processing multimodal information or a side effect of a complex multisensory processing system) or whether they are the result of experience. Regarding the latter case, some authors suggested that the putative non-arbitrary association might be the result of learning statistical regularities (e.g., objects located in elevated spatial position are also closer to the light source, hence brighter)[29,51]. **Study 2** aims to fill this gap by providing evidence of crossmodal correspondences in a very young animal (i.e., 3-day-old chicks were tested) in a fully controlled laboratory setting (i.e., chicks were hatched and reared in the lab until testing).

Interestingly, there is another circumstance in which a phenomenon similar to crossmodal correspondences occurs, i.e., space–number association (SNA). This is a natural tendency reported in several animal species[31,34,35] (including infants[32,33] and adult humans[52]) to associate small numbers to the left hemispace and large numbers to the right one. In fact, the SNA is explained as the result of an integrated mental representation of spatial and numerical information along a virtual left-to-right oriented line. However, in spite of the vast literature on the presence of such a spontaneous association, only a few studies explored whether SNA could support cognitive performance in unimodal-based tasks. According to the theoretical frame for multimodal integration proposed by Partan and Marler (1999), redundancy could either lead to the same or to an increased intensity of the original meaning[41], as the latter facilitates detecting and responding to the signal. In **Study 3**, baby chicks were tested in a numerical discrimination for which spatial information was present, though not relevant to solve the task (i.e., chicks had to locate the larger set, independent of its spatial position). The aim was to test whether chicks benefited from a redundancy between numerical and spatial information (i.e., the target set was on the right side) with respect to a condition when such a redundancy was absent (i.e., the target set was on the left side). The hypothesis is that, in spite of it being task-irrelevant, the spatial information would affect the processing of the task-relevant information (i.e., numerical), boosting performance in the congruent scenario. This would support the idea of spontaneous information integration as representative of an adaptive cognitive strategy employed by to facilitate processing the plethora of stimuli coming from their surroundings. Multimodal processing might indeed provide animals with a first low-demanding mechanism to organize and select the relevant information, increasing their chances of positive individual–environment interactions.

STUDY 1 – Long-term memory for multimodal visuospatial conditional information

Loconsole, M., Mascalzoni, E., Daisley, J. N., De Agrò, M., Vallortigara, G., Regolin, L., Lateralized declarative-like memory for conditional spatial information in domestic chicks (*Gallus gallus*). *Symmetry*, 13, e906. https://doi.org/10.3390/sym13050906

1. Introduction

As a precocial species, domestic chicks must be capable of interacting with the environment from the earliest moments of life[20]. The present work aimed to explore how chicks represent their surroundings and how they store these representations in the brain, testing whether 5-day-old chicks could spontaneously extrapolate a spatial-conditional rule from the environment and create an integrated memory on which to rely to solve a food-search task.

Studies on human subjects showed that we encode our explicit knowledge on the world in a dedicated memory storage system, namely declarative memory. We can consciously retrieve the contents of declarative memory and describe them in propositional forms[53,54]. We can rely on this memory for inferential reasoning, generalization, categorization, and planning[53–55]. A similar declarative-like memory system was also attested in other animal models, such as great apes (i.e., chimpanzees, gorillas, and bonobos)[56,57], rhesus monkeys[58], rats[59], jays[4,60], and domestic chickens[61]. For data on young subjects, Cozzutti and Vallortigara provided the first important evidence of a declarative-like memory system in 5-day-old domestic chicks[62]. They exposed baby chicks to two feeders located in two separated spatial locations (i.e., on the left and on the right in a rectangular arena) and filled with two different types of seeds. Chicks then underwent a devaluation phase, in which they were satiated with one of the two foods. At test, chicks selected the feeder containing the non-devaluated food, hence showing that they remembered the existence of the two food types and their different locations. Interestingly, the authors found a lateralization effect, for which chicks with both eyes in use and chicks with only the right eye (i.e., the left eye occluded via eye-patching) succeeded in locating the non-devaluated food. Chicks that were tested with only the left eye (i.e., the right eye occluded via eye-patching) behaved at chance level. The domestic chicken has a virtually complete optic chiasm decussation, each eye projecting mainly to the contralateral hemisphere[63,64]. This, together with the lack of a corpus callosum and a reduced interhemispheric crossover, allows for the study of brain lateralization effects by simply occluding one eye (i.e., monocular eye-patching) without the necessity of invasive procedures[63,65]. In their discussion, Cozzutti and Vallortigara provided two possible explanations to address chicks' reduced performance in the monocular-left test, which related to the way the information was encoded in the brain. A first possibility was that chicks had an already- integrated representation, but they showed a selective impairment in retrieving declarative-like information, due to a left hemispheric specialization. Alternatively, as the devaluation phase is separated from and subsequent to the exposure phase, it is possible that the two events (i.e., location of the different food types and food devaluation) were encoded separately and not in a whole integrated representation. In this latter case, the poor performance of left-eye chicks could be due to a left-hemisphere specialization in integration of information, rather than declarative-like memory per se.

The present study aims to address this issue by testing chicks in a food-searching paradigm with a visual–spatial conditional rule (i.e., if X, go A; if Y, go B). In this kind of paradigm, subjects experience all the required information in one single event (rather than two separate moments, as in Cozzutti and Vallortigara[62]), allowing them to create an already integrated memory. A lateralization effect, as reported in Cozzutti and Vallortigara[62], would indicate a true lateralization of declarative-like memory. Conversely, if both groups of monocular tested chicks succeed in the task, the lateralization effect shown by Cozzutti and Vallortigara[62] is more likely the result of a deficit in information integration.

2. Materials and methods

2.1. Subjects and rearing conditions

The study included 209 (107♂ and 102♀) chicks (*Gallus gallus domesticus*). Fertilized eggs were provided by a local hatchery (Agricola Berica, Montegalda, VI, Italy) and incubated and hatched in the laboratory at a controlled temperature (37.5 °C) and humidity (55–60%). Three days prior to hatching, the eggs were moved to a hatching machine at the same temperature and humidity, and exposed to the light. Upon hatching, subjects were feather-sexed and singly housed in standard metal cages (28 length × 32 width × 40 high cm), constantly lit by fluorescent lamps (36 W) placed 15 cm over the top of the cage (45 cm from the cage floor). A red plastic ball was hung in the centre of the cage at about 3 cm from the floor as a social enrichment[39]. Chicks' starter food was scattered close to the ball and replaced daily. Water was accessible ad libitum in a transparent jar adjacent to one of the sidewalls. The rearing room was maintained at a controlled temperature (30 °C) and humidity (68%).

2.2. Exposure

Exposure took place from day 2 to day 4. The experimental room, adjacent to the rearing room but acoustically isolated, was kept at a controlled temperature of 28 °C. Chicks were exposed to two environmental contexts (**Fig. 2A**), i.e., a blue or a yellow arena (28 × 32 × 40 cm). In each context, there were two panels (11 x 4 cm), each depicting a black geometrical shape, either a square or a cross, of approximately equal size (2 x 1.5 cm). For each chick, only one of the two shapes was rewarded (i.e., grain crumbs were hidden behind the panel). Each chick always experienced the S+ in the same spatial position in one context (e.g., always on the left in the blue arena) and in the opposite position in the other context (e.g., always on the right in the yellow arena). This allowed the subjects to associate one stimulus with the reward, with its position varying according to the context. Water was available ad libitum on a wall opposite to the panels. The rewarded shape and its position in each context were counterbalanced between subjects. On days 2 and 3 of life, the chicks were free to explore each arena for a total of 4 h per day (2 h in each arena). On day 4 of life, the exploration time was reduced to 2 h, with 1 h in each arena (**Fig. 2B**). For the remaining time, the subjects were housed in the home cages, as described in 2.1.

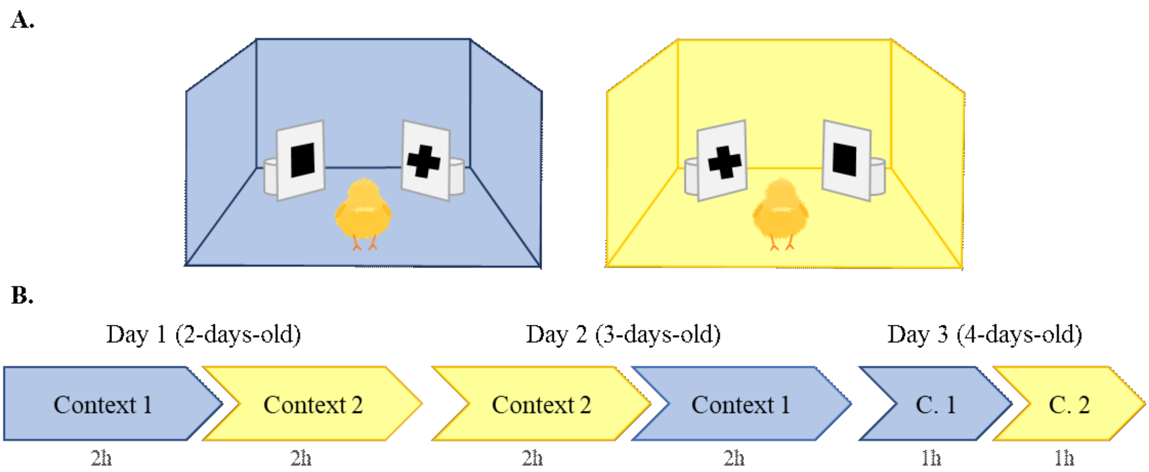


Fig. 2 Exposure: A. The two experimental contexts (i.e., blue and yellow arenas) with the two panels (each hiding a food jar). Only one of the jars was filled with food. Jars were not visible from the chick's starting point, and it needed to circumnavigate the panels to find them. For each chick, the shape associated with the food remained constant throughout the exposure (e.g., always the square), whereas its position (left or right) depended on the context (e.g., always on the left in the blue arena and always on the right in the yellow one). **B.** The exposure procedure. Chicks could explore each context for 4 h (2 h in each) on day 1 and day 2 of exposure (day 2 and day 3 of the chick's life), and for 2 h (1 h in each) on day 3 (day 4 of the chick's life). The first context explored by the chick (blue or yellow) was counterbalanced between subjects.

2.3. Eye-patching

Thirty min before test, chicks were randomly assigned to one of three possible experimental conditions (**Fig. 3**): i. binocular test (BIN; n = 71, 37♂), in which chicks were tested with both eyes in use; ii. right-eye monocular test (RE; n = 67, 32♂), in which the left eye was occluded, and chicks could only use their right eye; or iii. left-eye monocular test (LE; n = 71, 38♂), in which the right eye was occluded, and chicks could only use their left eye. Eye occlusion was realized with a removable, disposable, paper tape shaped like a cone so that, once applied on the bird's eye, it would obstruct vision without impairing normal blinking[65]. This is a well-established procedure, which allows for the study of hemispheric specialization in birds without resorting to invasive methodologies[63,65]. It is harmless for the chick and requires approximately 20 sec of animal handling. The experimenter handled BIN chicks for a similar amount of time to simulate the eye-patching procedure but without actual applying the patch.

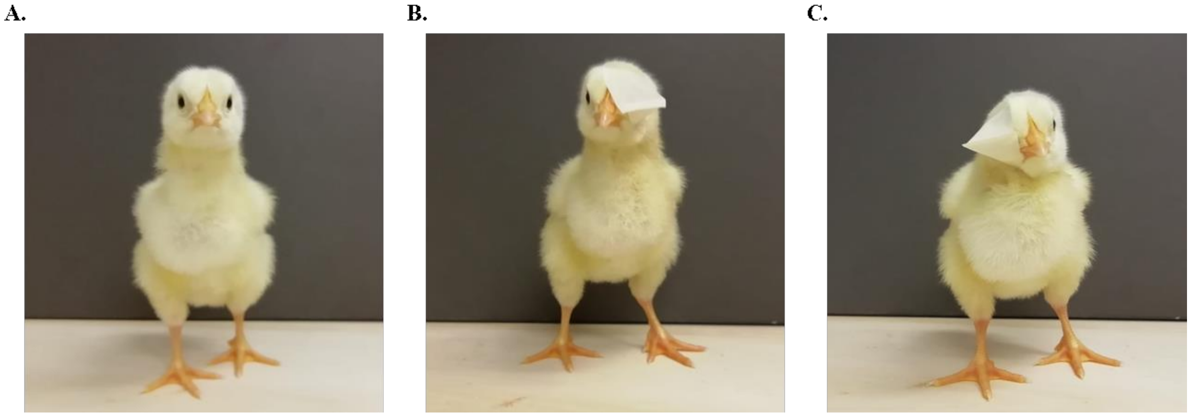


Fig. 3 Experimental conditions: A. Binocular condition (BIN): the chick was tested with both eyes in use; **B.** Right-eye monocular condition (RE): the chick's left eye was occluded, and vision was possible only with the right eye; **C.** Left-eye monocular condition (LE): the chick's right eye was occluded, and vision was possible only with the left eye.

2.4. Test

Chicks were tested on day 5 of life (**Fig. 4**). The experimental room was the same as for Exposure.

Each chick was placed for 6 min in one of two arenas used for exposure (i.e., either the yellow or the blue one). However, in this case, the rewarded shape was depicted on both panels, and there was no food reward. During the 6-min test, the chick's behaviour was recorded by a camera (Canon Legria HF R606), placed about 30 cm above the arena, and the behaviour was scored offline. The arena was virtually divided in three choice areas: a non-choice area (i.e., the chick's starting position), equidistant from both panels, and two choice areas (i.e., each comprised of the left or the right panel). The time spent in each choice area was considered a preference for that panel*spatial position combination. If such a combination was congruent with that experienced during Exposure, the chick's behaviour was scored as a correct choice; otherwise, it was scored as an error.

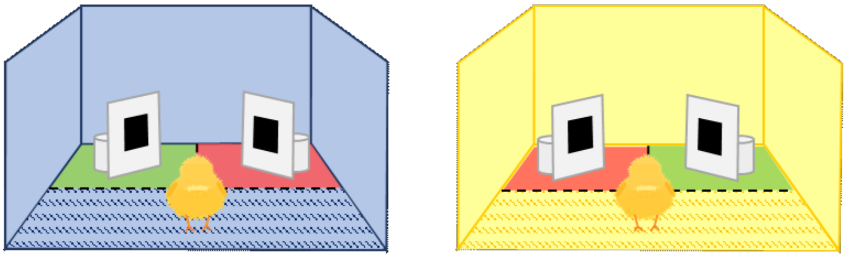


Fig. 4: An example of the test condition. In this case, the rewarded panel (i.e., the one hiding food during exposure) was the one depicting the square. At test, both panels showed the rewarded shape, and both hid empty jars. The arena was virtually divided in three areas (coloured for illustrative purposes). The dashed area indicates the chick's starting position, which was coded as a non-choice area. The time spent by the chick in the green area was coded as correct choice, as the spatial position of the S+ was congruent with that experienced during Exposure (in the case of this example, on the left in the blue arena and on the right in the yellow one, see **Fig. 2A**). The time spent by the chick in the red area was coded as an incorrect choice, as the spatial position of the S+ was incongruent with that experienced during Exposure. Chicks were randomly assigned to either the blue or the yellow context (counterbalanced between subjects).

2.5. Data analysis

The data were analysed in R version 4.0.2[66] using a multiple nested linear mixed effect model with a Gaussian error structure (using the R package lme4[67]).

First, an analysis was run using the overall time spent by the chicks in each choice area as a dependent variable. The independent variables were the stimulus value (i.e., correct or wrong with respect to the spatial conditional rule), the experimental condition (i.e., BIN, RE, or LE), the position of the stimulus (i.e., left or right), the context (i.e., blue or yellow), the stimulus shape (i.e., cross or square), the sex of the subjects (i.e., male or female), and the interaction between all these factors. Subjects were included in the model as the random effect. The best fitting model was selected by using an Akaike Information Criterion (AIC) based model selection.

A post hoc analysis with Bonferroni correction (using the R package emmeans[68]) was run on the resulting model to determine the effect direction of the predictors.

A second analysis was run on the chicks' first choice, i.e., which choice area the chicks approached at the beginning of the test. This was coded as binomial: 1 for approaching the correct area and 0 for approaching the incorrect area. A generalized mixed effect model based on the binomial curve was run, including the experimental condition (i.e., BIN, RE, or LE), the position of the correct stimulus (i.e., left or right), and their interaction. A post hoc multiple comparison analysis was then carried out on the model output. Graphs were realized using ggplot2[69].

3. Results

The model that resulted with the lowest AIC value (4825.8), which was the one that was consequently employed in the subsequent analysis, was the one containing the following predictors: stimulus value (i.e., correct or incorrect), experimental condition (i.e., BIN, RE, or LE), S+ position (i.e., left or right), context (i.e., blue or yellow), and their interactions.

There was no difference regarding the overall time spent close to either stimulus in the three experimental conditions (ANOVA, Sum. Sq. = 10330, Mean Sq. = 5165, F = 0.912, $p = 0.403$), suggesting that chicks' general activity levels were the same irrespective of them being assigned to the BIN, RE, or LE condition.

The analysis of the time spent in each choice area (i.e., congruent or incongruent with respect to the spatial conditional rule, **Fig. 5**) revealed a preference for the correct over the incorrect area for BIN (post hoc analysis, estimated difference between the averages [*est.*] = 47.182, *SE* = 12.6, *p* = 0.004) and RE chicks (post hoc analysis, *est.* = 57.05, *SE* = 13, *p* < 0.001), but not for the LE chicks (post hoc analysis, *est.* = −2.11, *SE* = 12.6, *p* = 1).

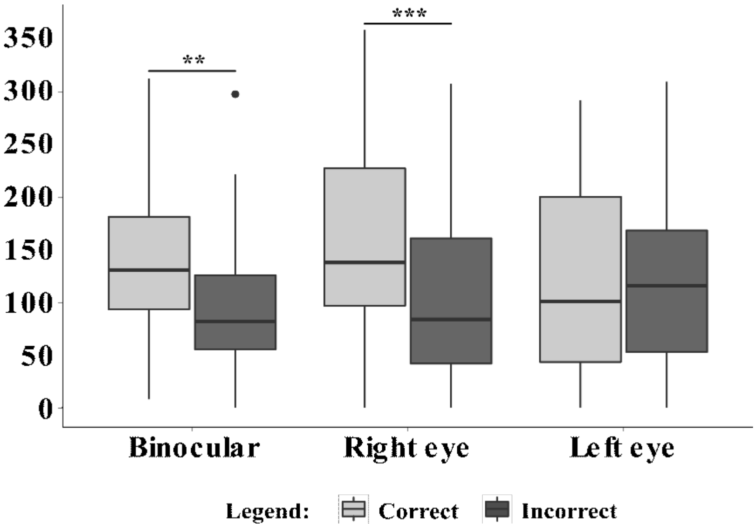


Fig. 5: Average time (sec) spent in the correct area (light grey) and in the incorrect area (dark grey) in each condition (i.e., BIN, RE and LE). Although BIN and RE chicks spent more time in the correct area (i.e., the one congruent with the previously experienced spatial conditional rule), LE chicks behaved at chance level. Asterisks indicate statistically significant contrasts: **p < 0.001; ***p < 0.0001.

For what concerns the interaction effects (**Fig. 6**), four factors were included in the final model. This caused the resulting subgroups to have reduced numerosities; hence, results must be interpreted with caution due to the low power of the analysis. Yet, LE chicks showed a preference for the incorrect area when the S+ congruent position was right and the context colour was blue (post hoc analysis, est. = −104.56, SE = 25.1, p < 0.001).

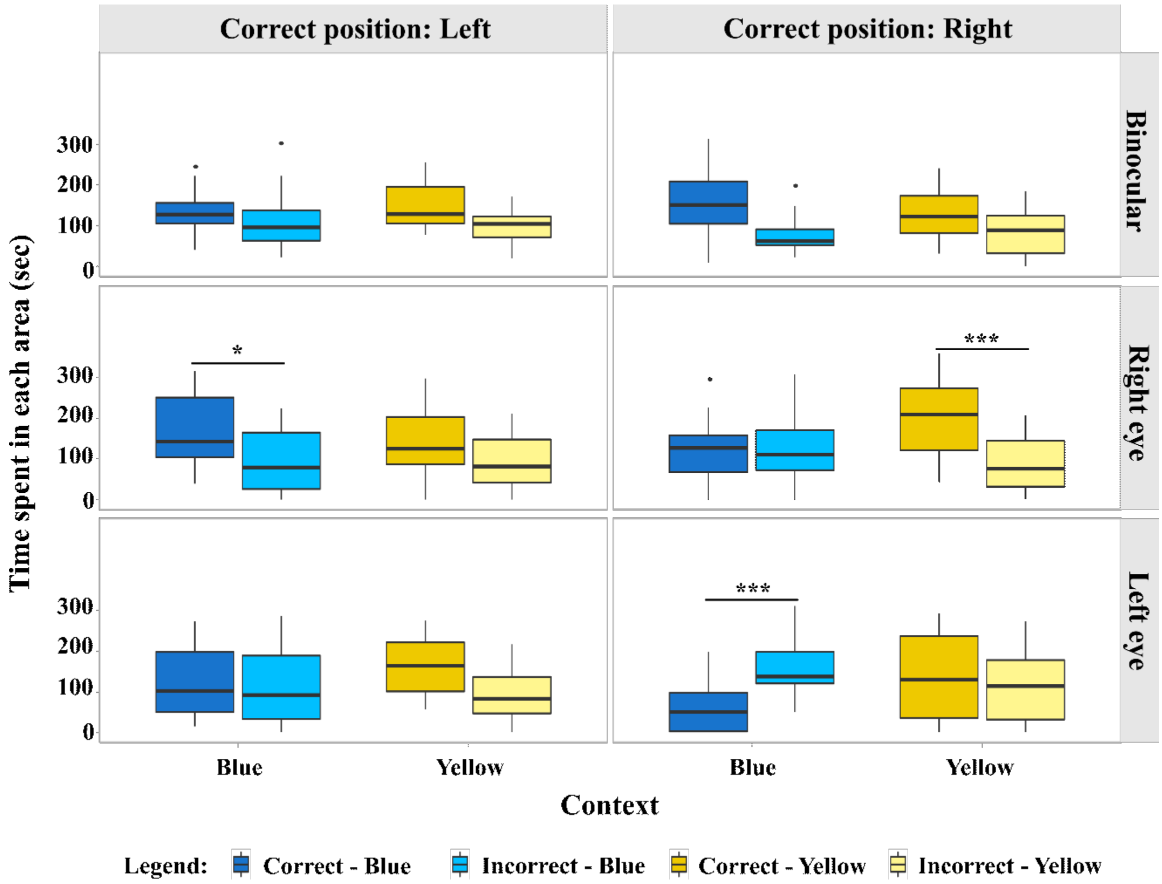


Fig. 6: Time (sec) spent in the correct choice area (dark blue and dark yellow) or incorrect choice area (light blue and light yellow) for each experimental condition (i.e., BIN, RE, or LE), separately illustrated for correct position (left or right) and colour of the arena (blue or yellow). Dark blue indicates time spent in the correct choice area in the blue context; light blue indicates time spent in the incorrect choice area in the blue context. Dark yellow indicates time within the correct area in the yellow arena; light yellow indicates time spent within the incorrect area. Asterisks indicate statistically significant contrasts: **p < 0.001; ***p < 0.0001.

Concerning the analysis of the chick's first stimulus approach at the beginning of the test, no preference emerged in any of the three experimental conditions (Exact binomial test. BIN: success = 33; total = 71; prob. = 0.465; p = 0.635; RE: success = 40, total = 67, prob. = 0.597, p = 0.142; and LE: success = 36; total = 71, prob. = 0.507, p = 1).

4. Discussion

This study aimed to assess the nature of integrated declarative-like memories, as well as a possible brain lateralization for memory retrieval. Results showed that chicks could process multimodal information from the environment and create an integrated representation of a visuospatial conditional rule. Eventually, they can retrieve such an integrated representation to solve a food-searching task. Yet, chicks failed in the task when tested with only the left eye in use (i.e., right hemisphere processing), supporting the idea of a left hemispheric specialization for declarative-like memory. Previous studies showed that young chicks could successfully perform tasks that required acquisition of relational rules[70], information integration[71], or generalization[72]. However, chicks underwent dedicated training sessions[70,72] or were tested only for their working memory, with all the required information constantly available in the surrounding environment[71]. In the present study, chicks spontaneously encoded the conditional rule, suggesting a predisposition to form explicit (i.e., declarative-like) integrated memory even in the absence of formal training. This is impressive, considering that adult pigeons require a minimum of 6-months extensive training (or fail) to acquire a similar spatial conditional rule (i.e., geometric shape and up/down spatial position[73]). A possible explanation could be that chicks are subject to different evolutionary pressures because, as a precocial species, they need to interact autonomously with the environment from the earliest stages of life[20]. It is yet to be determined whether such a mechanism follows a different developmental trajectory in altricial species. Studies on 6-month-old infants have suggested a similar early development of declarative memory, however in such a case, the system is still immature and inflexible[74,75].

The chicks remembered the conditional rule and used it at test (i.e., in a moment subsequent to exposure, in which the previously available contextual information was partially removed) further supports the presence of long-term memory for past events in baby chicks. In fact, chicks successfully created an integrated representation of their experiences (i.e., exposure) and stored this in a long-term (declarative) system. This mechanism appears to be subject to a left hemispheric specialization. Chicks tested in the BIN or RE condition succeeded in retrieving the integrated memory, but chicks tested in the LE condition failed and behaved at chance level. These results complement those by Cozzutti and Vallortigara[62], clarifying the nature of the stored declarative-like representation and the role of brain lateralization. In the present study, subjects were exposed to the conditional rule within one single event, allowing them to create a whole, already-integrated, memory engram. If failure in the original study[62] was the result of left hemispheric specialization for information integration, such an impairment would have disappeared in the present study, during which information integration took place previous to the test and in a binocular condition. Conversely, LE poor performance was confirmed in the present study, which suggests a sheer left hemispheric specialization for declarative-like memory retrieval. This is in line with data from adult birds that showed a brain lateralization for storing and retrieving task-contingency information[73,76–78].

Although the chicks' general performance in the three experimental conditions was in line with the study aims and with previous literature, some unforeseen minor effects were also noticed. In fact, LE chicks showed a preference for the incorrect choice area when the S+ was on the right side in the blue context. A first possible explanation is that of an attentional bias for the left hemispace resulting from the eye-patching procedure, as a tendency towards the incorrect area (even though it is not significant) could also be seen for LE with the S+ on the left side in the yellow context. Another possibility is related to a colour-based bias. In fact, in spite of chicks having a spontaneous preference for the orange and the blue regions of the colour spectrum[79,80], there were cases in which they showed avoidance of the colour blue[81]. It is not possible to exclude that, in the present study, a similar avoidance-reaction was heightened by right hemispheric processing, causing an unpredictable modification of chicks' behaviour.

Lastly, first choice at test did not predict chicks' general performance, as in all experimental conditions chicks' first approaches were random. It is possible that subjects initially relied only on the sight of the rewarded stimulus (as at test it was depicted on both panels), thus choosing at chance level. Subsequently, as their behaviour did not lead to the expected outcome (i.e., they did not find any food reward, as it was not present), they recalled and relied on the declarative-like memory of the exposure phase, thus also retrieving the information regarding the visual–spatial conditional rule. If the retrieving process was successful (i.e., as for BIN and RE chicks), subjects could address their behaviour according to the integrated memory engram, resulting in their general performance being above chance level. If the retrieving process failed (i.e., as for LE chicks), subjects could not access the conditional rule and, consequently, kept exploring both areas equally. Following this line of reasoning, it is possible to hypothesize that, despite chicks being able to create integrated memories of past events spontaneously, the recollection process is not immediate, taking place only when other, simpler (i.e., remembering only the rewarded shape) strategy results are inefficient.

STUDY 2 – Space–luminance crossmodal correspondences in 3-day-old chicks

Loconsole, M., Pasculli, M. S., Regolin, L., Space-luminance crossmodal correspondences in domestic chicks. *Vision Research*, 188, 26-31. https://doi.org/10.1016/j.visres.2021.07.001

1. Introduction

In spite of the absence of any explicit rule, we associate non-redundant information from different sensory modalities, a phenomenon known as crossmodal correspondences[21]. For instance, we match luminance and auditory pitch[22,82] or odours and shapes, with lemon scent being linked to spiky shapes and vanilla scent to round shapes[23]. Crossmodal correspondences were also confirmed in preverbal infants[28,83], supporting the idea of these being a predisposed component of perception. However, no conclusive evidence is available, as the ontogenetic development of such a mechanism is still debated. In fact, as the youngest group tested was 1- to 3-month-old infant [27,28], it is impossible to eliminate completely the role of fast post-natal learning[28,29,84].

Crossmodal correspondences are not a human prerogative and have been reported in other mammalian species[85]. Chimpanzees pair luminosity (i.e., black and white squares) with auditory pitch (i.e., low and high sounds, respectively)[22], whereas rhesus monkeys associate the spatial position of an object (i.e., closer or further) with auditory pitch (i.e., low and high sounds, respectively)[26]. Similar to monkeys, dogs associate spatially elevated visual stimuli with high auditory pitches, and stimuli located in a lower spatial position with low pitched sounds[24]. For instance, in the pioneering study by Ludwig and colleagues (2011) 33 adult humans and 6 chimpanzees were tested in the same classification task, where they had to respond whether a square presented on a monitor was black or white. During each trial a task-irrelevant background audio was played, either having a high- or a low- pitch. Both humans and chimpanzees were faster when they had to respond to white squares when hearing the high-pitch sound and to black squares when hearing the low-pitch sound. This was interpreted as a facilitation effect due to the congruency between the two multimodal information according to pitch-luminance crossmodal correspondences. Altogether, the data suggest a shared origin of crossmodal correspondences, at least within the mammalian clade.

By studying young chicks, it would be possible to shed light on the ontogenesis (i.e., how early are they available during development, and the role of the experience on their appearance) and the phylogenesis (i.e., is there an analogous mechanism in clades other than mammals) of such a phenomenon. Chicks (*Gallus gallus*) can be considered the most suitable model to answer these questions. They are a precocial species, thus they allow for the study of perceptual and cognitive mechanisms from the earliest stages of life in a fully controlled laboratory environment[17,20]. In addition, they were shown to create integrated representation of multimodal information spontaneously [62,86]. This work aims to investigate the presence of crossmodal correspondences in 3-day-old chicks, with respect to the space–luminance association[50]. Adult humans show a facilitation effect due to a predisposition to associate spatial and luminance information. When humans had to judge whether a test stimulus had a higher or lower luminosity than a target stimulus, participants performed better (i.e., higher accuracy and faster reaction times) when they had to respond to low luminosity with the left hand and to high luminosity with the right one, indicating a crossmodal association between these two dimensions. In the present study, baby chicks were presented with a similar association, i.e., to obtain a food reward, they could choose between two identical panels (either both black–low luminance or both white–high luminance), one placed on the left and one on the right side of a grey arena. If baby chicks do possess a crossmodal association similar to humans, they should preferentially approach the left dark panel and the right white panel. This would support the idea of crossmodal correspondences being an early available, experience-independent mechanism widespread across different species.

2. Materials and methods

2.1. Subjects and rearing conditions

The subjects were 79 male domestic chicks. Fertilized eggs were provided monthly by a local hatchery (Incubatoio La Pellegrina, San Pietro in Gu, PD, Italy) and incubated in the laboratory at a controlled temperature (37.5 °C) and humidity (55–60%). Three days prior to hatching, the eggs were moved to a hatching machine at the same temperature and humidity, and exposed to the light. Each week one batch of approximately ten eggs was hatched. Upon hatching, the chicks were feather sexed, and the males were housed in pairs in standard metal cages (28 length × 32 width × 40 hight cm) lit by 36 W fluorescent lamps placed 15 cm over the top of the cage. Only males were used in this study as they are more motivated to work for a food reward (as in the case of this study) than female chicks[87]. This would reduce behavioural variability and reduce the risk of having to discard subjects because of their poor motivation in engaging the task.

Cages were lit from 7 a.m. to 7 p.m. followed by 2-/3-h blocks of dark/light alternation from 7 p.m. to 7 a.m. Water and food were available ad libitum in transparent jars placed on the cage's wall. Chicks were fed some mealworms (*Tenebrio molitor* larvae) daily as supplemental nutrition. Mealworms were also used as a food reward during testing; thus, chicks that refused to eat them during rearing (3% of the subjects) were automatically discarded from the study.

On day 3 of life, the chicks were randomly assigned to the control or experimental condition. The chicks were deprived of food for one hour prior to the experimental procedure to maintain an optimal level of motivation for the food reward. Water remained available all the time. It is important to note that from the moment of hatching and throughout the rearing period, the chicks were never exposed to the experimental stimuli (i.e., grey, black, or white panels, see 2.2 and 2.3), nor did they have the chance to associate luminosity with food (i.e., food and water bowls within the rearing cage were made of transparent glass, and the rearing cages were made of opaque sanded metal).

2.2. Training

Training was identical for all subjects, regardless of them being in the control or experimental condition. Each session lasted about 20 min and was immediately followed by a test. Training was aimed at acquainting the chick with the experimental arena and teaching it to circumnavigate a panel to find a food reward, i.e., half a mealworm. The experimental arena (**Fig. 7**) was constructed as a grey plastic triangle (76 cm long × 32 cm high). A removable glass partition placed across one corner of the arena created the starting area in which the subject was placed before the beginning of each trial (**Fig. 7D**). Perpendicular to that, a vertical partition (25 × 37 hight cm) divided the other end of the arena in half. During training, a grey panel (12 length × 3.5 width × 15 hight cm) was placed in front of the vertical partition (**Fig. 7A**). The food reward was hidden behind the panel, out of the chicks' sight. The chick was then placed in the starting position and held there for a few seconds. After the glass partition was removed, the chick was free to explore the arena. If it did not spontaneously go behind the panel within 3 min, it was lured towards the panel with a dummy mealworm hung from a transparent fishing line. The training was considered complete after the chick promptly circumnavigated the panel three consecutive times. In the experimental condition, the chicks underwent four additional trials after completing the training, two trials in which they were presented with a white panel and two trials in which they were presented with a black panel, in alternating order. As for the training with the grey panel, one panel was presented in front of the chick in the middle of the arena (and in front of the vertical partition). These additional trials were required to acquaint the chick with the presence of a black or white panel but to avoid exposing it to combinations of spatial positioning and luminance (which would instead be experienced for the first time during testing).

2.3. Test

Testing took place immediately after training. The arena was the same as that used for training, with the only difference being that now chicks were presented with two panels at once, each placed in one of the two halves created by the vertical partition. Testing consisted of 20 consecutive trials in which the chick was free to approach either panel (Each panel rewarded the chick with half a mealworm). As soon as it had retrieved the food reward from behind the chosen panel, it was immediately removed from the arena, without the possibility of approaching the other panel, and the subsequent trial was started. In the control condition, the chicks could choose between two identical grey panels (**Fig. 7B**). In the experimental condition, the chicks could choose between two identical panels of either high (white) or low (black) luminance (**Fig. 7C**) that were used in a pseudorandom presentation order, with the same luminance never occurring in more than two consecutive trials. The luminance (black/white) of the panel presented in the first trial was counterbalanced between subjects.

The entire test was video recorded by a camera (Canon Legria HF R606) placed at about 30 cm from the top of the arena, allowing for offline scoring of the spatial position (left/right) of the panel chosen by the chicks.

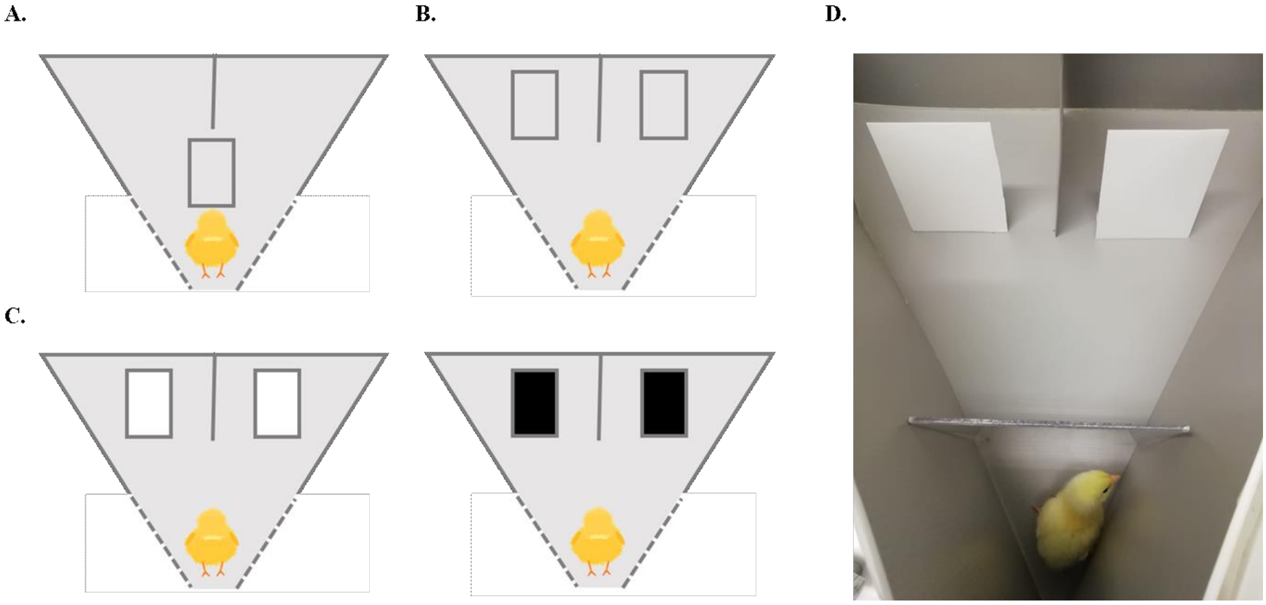


Fig. 7 Training and test conditions: A. Training condition. One grey panel was placed in the centre of the arena, in front of the chick. For the chicks from the experimental condition, four additional trials were held. All trials used the same setting, with the only exception being the colour of the panel (two trials with a single black panel alternated with two trials with a single white panel,). **B.** Test for the control condition. Chicks underwent 20 trials, all with two identical grey panels. **C.** Test for the experimental condition. Chicks underwent 20 trials, 10 with two identical white panels and 10 with two identical black panels, in a pseudorandom order (i.e., the same luminosity never occurred more than two subsequent times). **D.** The chick restrained by the glass partition in the starting area (this example was for a test trial from the experimental condition, with two white panels).

2.4. Data analysis

Data were analysed using the statistical software R, version 4.0.2[66]. With the dependent variable being dichotomous (i.e., spatial position of the chosen panel: left / right), a generalized linear mixed-effect model with a binomial structure was used. The subjects were included in the model as random effects. The goodness of fit was checked using the R package DHARMa[88]. A post hoc analysis with Bonferroni correction (using the R package emmeans[68]) was run to test the chicks' performance in each condition against the chance level.

A second analysis was conducted on the first six trials and the last six trials of only the testing. This was done to explore the presence of an effect resulting from each chick undergoing multiple consecutive trials, which could have affected their performance[89]. If the chicks demonstrated the crossmodal association in the first block of trials, it would be possible to exclude learning throughout the testing. Conversely, if the chicks were learning to associate spatial and luminance information through the test, a more pronounced effect (i.e., more choices of right–white and left–black panels) should appear in the final block of trials. Lastly, if the effect weakened in the last block of trials instead, this would indicate a progressive loss of motivation and/or attention, suggesting the chicks were not sufficiently engaged in the task and may even behave randomly towards the end[89]. All graphs were generated using ggplot2[69].

3. Results

In the control condition (**Fig. 8A**), the chicks did not show any spatial preference and approached both panels at the chance level, post hoc analysis: P(approach the panel on the right) = 0.54, $SE = 0.04$, $z = 0.98$, $p = 0.33$. In the experimental condition (**Fig. 8B**), an effect of the luminance of the stimuli was found, GLMM analysis of deviance: $X^2(1, N = 40) = 26.09$, $p < 0.001$, for which the chicks presented with two black panels (low luminance) preferentially approached the one in the left hemispace, post hoc analysis: P(approach the panel on the right) = 0.41, $SE = 0.04$, $z = -2.07$, $p = 0.04$, while the chicks presented with two white panels (high luminance) preferentially approached the one in the right hemispace, post hoc analysis: P(approach the panel on the right) = 0.61, $SE = 0.04$, $z = 2.58$, $p = 0.01$.

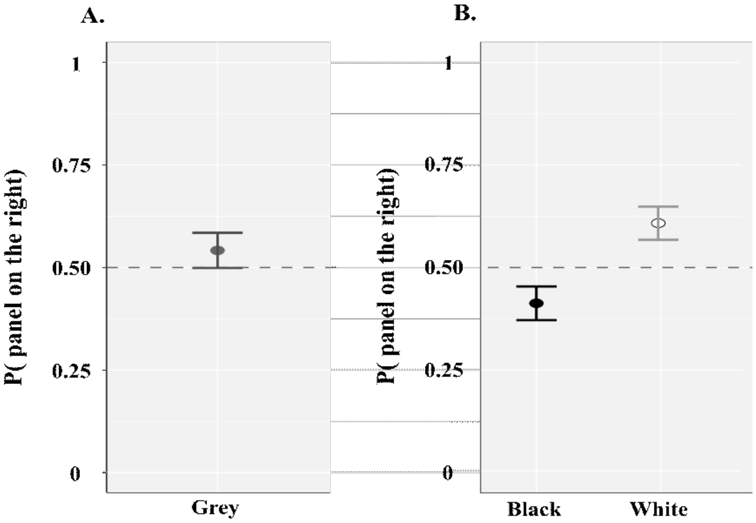


Fig. 8 Probability of chicks choosing the panel on the right: The y-axis shows the probability (from 0 to 1) of choosing the panel on the right side of the arena. The bars represent standard error; the dashed line represents the chance level (y = 0.5). **A.** Control condition, in which the chicks were tested with two identical grey panels. **B.** Experimental condition, in which the chicks were tested with two identical black panels or with two identical white panels in alternating order.

Previous studies that employed a paradigm in which chicks were tested in multiple consecutive trials with a binomial choice reported an effect from the repeated trials. Birds' performance decreased during the test, indicating a loss of attention and/or motivation[40,89]. In the case of the present study, the performance of the chicks tested in the control condition (**Fig. 9A**) remained at the chance level in the first six trials, post hoc analysis: *P*(approach the panel on the right) = 0.56, *SE* = 0.05, $z = 1.24$, $p = 0.21$, and the last six trials, post hoc analysis: *P*(approach the panel on the right) = 0.53, *SE* = 0.05, $z = 0.54$, $p = 0.59$. In the experimental condition (**Fig. 9B**), the space–luminance crossmodal correspondence emerged in the analysis of the first six trials, similar to what was reported for the general performance: the chicks preferentially chose the right white panel, post hoc analysis: *P*(approach the panel on the right) = 0.65, *SE* = 0.05, $z = 2.53$, $p = 0.01$, and the left black panel, post hoc analysis: *P*(approach the panel on the right) = 0.36, *SE* = 0.05; z = −2.48, $p = 0.01$. However, such an effect disappeared in the analysis of the last six trials, where the chicks behaved at the chance level, post hoc analysis, two white panels: *P*(approach the panel on the right) = 0.56, *SE* = 0.06, *z* = 0.99, *p* = 0.32; two black panels: *P*(approach the panel on the right) = 0.43, *SE* = 0.06, *z* = −1.14, *p* = 0.25.

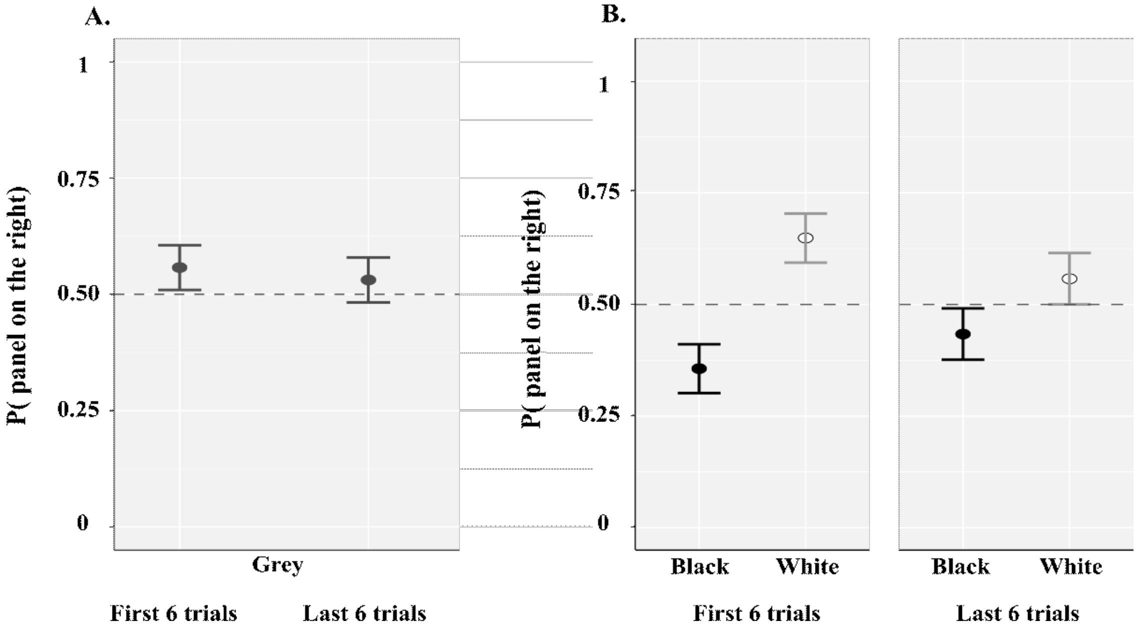


Fig. 9 Analysis of the first six and last six trials: The y-axis shows the probability (from 0 to 1) of choosing the panel on the right side of the arena. The bars represent standard error; the dashed line represents the chance level (y = 0.5). **A.** Control condition, in which the chicks were tested with two identical grey panels. The chicks behaved at the chance level in both the first six and the last six trials. **B.** Experimental condition, in which the chicks were tested with two identical black panels or with two identical white panels in alternating order. The chicks showed crossmodal correspondence in the first six trials; however, it disappeared in the last six trials, where they chose at random.

4. Discussion

This study explored the presence of a case of crossmodal correspondences, namely a space–luminance association[50], in young chicks. Similar to what has been reported in humans, the chicks showed a spontaneous association between the left hemispace and low luminance stimuli (i.e., they preferred to circumnavigate the left black panel) and between the right hemispace and high luminance stimuli (i.e., they preferred to circumnavigate the right white panel). This result expands the present knowledge on crossmodal correspondences, providing important insights on the origin of this mechanism from both phylogenetic and ontogenetic points of view. In fact, all previous studies that investigated crossmodal correspondences were focused on humans and other mammalian species. Evidence from a more distantly related clade (i.e., birds) relates to two hypotheses. On one hand, crossmodal correspondences might date back to a shared common ancestor, before birds diverged from mammals (i.e., approximately 300–320 million years ago[90,91]). Alternatively, crossmodal correspondences might represent a case of convergent evolution[92], having evolved separately in birds and mammals leading to similar selection pressures. This hypothesis is supported by the fact that both mammals and birds deal with a similar constantly mutating environment, and they might benefit from a low-cost mechanism for the fast processing of information coming from different sensory modalities. If this was the case, we could hypothesize that crossmodal correspondences could be found in animals other than mammals and birds that are also known to rely on multisensory perception (e.g., reptiles and insects). Further studies are required to test this hypothesis.

Regarding ontogeny, data on human infants has suggested a possible early emergence of crossmodal correspondences, despite the impossibility of completely ruling out the role of postnatal learning (see Introduction). Studies on non-human primates have not been conclusive either[29]. The two biggest concerns stem from the fact that animals live in uncontrolled environments that could constitute a source of confounding (e.g., light sources, enrichments) and from the extensive training to which animals are subject before testing (causing them to be largely exposed to the experimental stimuli and testing procedures). In the case of the present study, both these factors were carefully considered. The chicks were hatched in a laboratory and reared in a fully controlled environment, in which they never had a chance to associate luminosity and spatial information. In addition, the employed paradigm did not require any preliminary exposure to the testing stimuli or extensive training for the animals to learn the experimental procedure. This strongly supports the idea of crossmodal correspondences being an early available mechanism that requires no dedicated experience. Ideally, such a mechanism must be in place at the very early stages of development as it holds a certain adaptive value.

Data from human infants showed that they can rely better on unimodal sensory stimulation (visual, such as a caregiver's face, or acoustic, such as a caregiver's voice) if they were first exposed to a bimodal presentation of both[49,93]. A similar effect was also reported in non-human animals: domestic dogs reactivate a visual representation of the owner's face when hearing their voice[94], while both horses[95] and rhesus monkeys matched[42] a heard call with a specific individual from the group, even though the individual was not in their visual field. Hence, crossmodal associations might facilitate the subsequent multisensory information that animals employ to face different environmental situations.

Another possible evolutionary advantage that comes from possessing a crossmodal associative mechanism is that of a first low-cognition demanding pathway for processing the plethora of information that would otherwise be overstimulating. This could explain the difference in performance that emerged in the present study when analysing the first six and last six trials. The results of this analysis (i.e., the crossmodal effect being present only in the first six trials in the experimental condition) excluded the possibility of experience-driven learning. On the other hand, they showed a modification in the chicks' behaviour possibly due to a loss in motivation and/or attention. This is unlikely due to fatigue (as reported in a previous study with a similar two-alternative-choice task[89]) as the test is relatively fast (about 20 min) and the choice is always rewarded. Interestingly, it could be the case of the task being excessively easy for the chicks, which soon learnt that both stimuli equally led to a reward and thus ceased to process them (resulting in the loss of the crossmodal effect). This would indicate that crossmodal correspondences might constitute a first strategy employed by animals when facing a novel situation and which is subject to habituation or learning.

STUDY 3 – Numerical discrimination is supported by congruency between spatial and numerical information

Loconsole, M., Rugani, R., Regolin, L. *In Preparation.*

1. Introduction

Numerical competences are widespread among different species, playing a key role in adaptation and survival[96]. Domestic chicks are one of the most used model for the study of numerical cognition in non-human animals, due to chicks' high sensitivity and responsivity to numerical information[19]. They have been shown to be able to master a variety of numerical tasks, such as using ordinal information[97,98], proportions[72], and proto-arithmetic operations[39,99]. For instance, 3- and 4-day-old chicks were reported to spontaneously (i.e., in the absence of any numerical training) discriminate between two sets of elements, either with small[99–101] or large[101,102] numerosities. After being imprinted with some artificial objects (chicks were individually reared with these objects up to the day of testing), chicks were presented with two subsets of such objects, hidden in separate spatial locations. Chicks could successfully discriminate between the numerosities of the two subsets and showed a high motivation to re-join the larger one.

Interestingly, chicks have also been shown to possess a peculiar case of multimodal association between spatial and numerical information, for which they associate smaller numerosities with the left hemispace and larger numerosities with the right one[34,35]. This is known as a spatial–numerical association (SNA) effect and has been explained in terms of a predisposed association between numbers and spatial positions, represented in a left-to-right oriented mental number line[103,104]. The existence of the SNA and the fact that it might be a precocious and spontaneous mechanism is supported by several studies on preverbal infants[32,105] and non-human animals[30,72,106]. In the original study that showed the presence of SNA in baby chicks, the birds learnt to retrieve a food reward behind a central panel depicting five elements. During testing, the chicks were presented with two panels, one on their left and one on their right. When the two panels depicted two elements each (i.e., a numerosity smaller than that experienced at training), the chicks preferentially chose to circumnavigate the left panel. When the two panels depicted eight elements each (i.e., a numerosity larger than that experienced at training), the chicks chose the right panel[34,35]. It is worth noting that the chicks spontaneously associated spatial and numerical information even though it was not necessary to solve the task (i.e., they were not rewarded during testing; thus, there was no "correct choice"). However, it might be the case of the experimental design prompting the emergence of the SNA. In the absence of numerical information (i.e., the two panels both depicted the exact same numerosity, which was different from the one previously associated with the food reward), the chicks might have relied on the spatial information and chose the panel where this was congruent with the numerical magnitude (i.e., smaller or larger) of that experienced at training. It is yet to be determined whether such an association would remain in even more complex tasks where chicks are provided spatial and numerical information together. To date, only one study has tried to answer this question, showing the SNA effect in a proto-arithmetic task in 4-day-old chicks[107]. After being imprinted with the testing objects, the chicks were presented with the 5 vs 10 or 6 vs 9 comparisons, wherein each element of the set was individually presented and made to disappear behind one of two identical opaque panels (one on the left and one on the right of the chick). Under this condition, the chicks should preferentially re-join the larger set[99–102] (i.e., 10 or 9, respectively). In fact, the chicks were better at locating the larger set when it was behind the right panel, the first important evidence of SNA supporting performance in a numerical discrimination task.

The present study aimed to test the extent to which chicks SNA could boost their performance and whether it is subject to constraints due to cognitive overload. Indeed, 5 vs 10 and 6 vs 9 are relatively easy comparisons for the baby chicks, as they both have quite a large ratio. This is the fraction between the larger and the smaller set in a numerical comparison, and it indicates the difficulty of discriminating between the two sets (as the ratio approximates 1, the difficulty of the discrimination increases)[19,89,102]. In the case of 5 vs 10 and 6 vs 9 comparisons, the ratios are 0.5 and 0.67, respectively. It is yet to be investigated whether chicks also can rely on the SNA when facing a more complex discrimination that implies a higher effort in terms of both calculation and working memory, such as the 3 vs 4 comparison. This is considered a critical comparison in numerical studies of both human infants[108–110] and adult non-human animals[111–114]. Similarly, domestic chicks were reported to fail the 3 vs 4 comparison, unless their performance was supported by additional cognitive strategies (i.e., grouping[89] or individual object processing[40]). Herein, the data from a previous study on 3 vs 4 discrimination in 4-day-old chicks are recoded and analysed to test for the presence of the SNA effect. The original study from which the behavioural data were obtained aimed to investigate the role of individual processing of face-like stimuli in numerical discrimination[115]. Chicks were reared with a set of seven objects as artificial social companions and eventually tested with the 3 vs 4 comparison. The chicks could be assigned to one of four possible experimental conditions, each differing in the characteristics of the rearing or testing stimuli (see 2.3 and 2.6). On day 4 of life, the chicks were presented with the proto-arithmetic comparison 1 + 1 + 1 vs 1 + 1 + 1 + 1 with the same paradigm as that previously employed for the 5 vs 10 and 6 vs 9 comparisons[101]. Each chick underwent 20 test trials where the largest set was made to disappear (with a one-by-one presentation of the stimuli) either behind the left or the right panel, in a pseudorandom order (i.e., it never disappeared in the same position more than two consecutive times). To solve the task, the chicks had to keep track of each object, create a mental representation of each set and its location, and compare the two sets. If the chicks spontaneously map magnitude from left to right, they should show a facilitation effect in those trials in which the larger set is hidden behind the right panel, as was found in the previous study[107] (i.e., independent of the difficulty of the task). On the other hand, if SNA facilitation results from a top-down process that chicks could actively implement in specific circumstances, it should not be present when chicks are already dealing with a high-cognition demanding task.

2. Materials and methods

2.1. Subjects and rearing conditions

The study was conducted on 59 female domestic chicks (*Gallus gallus*). Fertilized eggs were provided by a local hatchery (Incubatoio La Pellegrina, San Pietro in Gu, PD, Italy) and incubated in the laboratory. Three days prior to hatching, the eggs were moved to a hatching machine at the same temperature and humidity, and exposed to the light. The rearing room and cages were the same as those described in **Study 1** and **Study 2**. Upon hatching, the chicks were individually placed in the rearing cage with seven two-dimensional stimuli. The chicks remained in the home cage with the rearing stimuli from the morning of hatching to the day of testing, i.e., for approximately 78 h. The characteristics of the stimuli depended on the experimental condition to which each chick was assigned (see 2.3).

2.2. Experimental stimuli

The experimental stimuli (**Fig. 10**) consisted of seven two-dimensional pieces of laminated orange cardboard with three black inner features of different geometrical shapes. These were hung on transparent threads approximately 3–4 cm from the cage floor and 2 cm apart from each other (**Fig. 10A**). The cardboard was shaped so that it had an upper oval part (4 hight × 3.25 width cm) placed on a rectangular base (2 hight × 1.5 width cm). Within the oval, three black geometrical shapes were arranged to resemble a face-like pattern: i.e., two upper dark areas (“eyes”) and one mid–lower dark area (“mouth”/“beak”). The chicks were shown to be highly sensitive to such a configuration, which elicited a strong social response[116]. The stimuli were made so that each one was different by employing different geometrical shapes for the inner features and by changing the eye-to-eye and eyes-to-mouth distances (**Fig. 10B**). In Condition 4, the rearing stimuli consisted of the outline only, with no inner features.

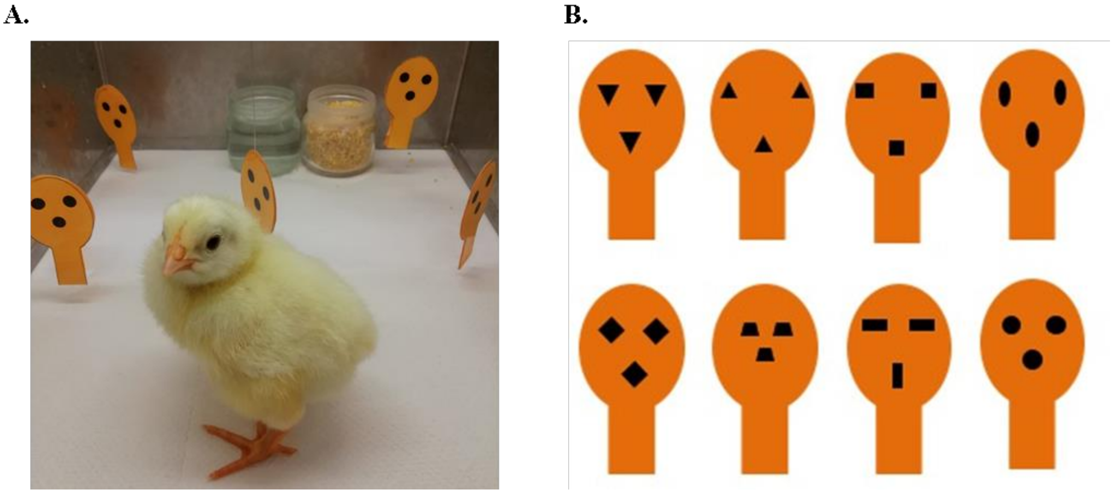
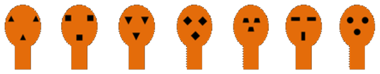
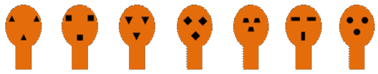
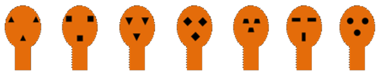


Fig. 10 Experimental stimuli: A. The chick in the cage with the two-dimensional stimuli used as rearing companions. In this example, the chick was reared with seven identical copies of one stimulus (Condition 2 and Condition 3). The geometrical shape of the inner features changed between subjects. **B.** An example of the different shapes used for the experimental stimuli. In Condition 4, the rearing stimuli had no inner features and consisted of the silhouette only.

2.3. Experimental stimuli

The four experimental conditions differed regarding the characteristics of the rearing or testing stimuli (**Tab. 1**). Each condition targeted a specific aspect of individual recognition as a potential cognitive strategy to support numerical discrimination. However, this was not relevant for the present study, which instead aimed to exploring the presence of the SNA facilitation, regardless of the experimental manipulations. For a detailed description of the experimental hypothesis for each condition, please refer to the original study[115].

Experimental Condition	**Rearing (7 stimuli)**	**Test (1+1+1 vs 1+1+1+1)**
Cond. 1 (n = 14)	Individually different 	Individually different (same as rearing) 
Cond. 2 (n = 15)	Identical copies 	Identical copies (same as rearing) 
Cond. 3 (n = 15)	Identical copies 	Individually different (all novel) 
Cond. 4 (n = 15)	Silhouette only 	Individually different 

Tab. 1 The experimental conditions: Whereas the rearing, training, and testing procedures remained unvaried, the experimental conditions differed from one another regarding the characteristics of the stimuli used during rearing or training and testing. When the chicks were reared with seven copies of one stimulus (Cond. 2 and Cond. 3), each subject was randomly assigned to one of the eight possible stimuli (differing for the shapes of the inner features, see **Fig. 10B**).

2.4. Training

Training took place in an experimental arena as described for **Study 1** and **Study 2**. The chick was placed in a circular arena (95 cm circumference, 30 cm high) within a holding box (10 width × 20 length × 20 hight cm) adjacent to the wall of the arena (**Fig. 11**). This represented the chick's starting position. The side of the holding box facing the centre of the arena consisted of a removable glass partition, allowing the chicks to watch the stimuli displayed within the arena. In front of it, at a distance of approximately 25 cm, was placed an opaque panel (16 hight

× 10 width cm). The chicks had to learn to circumnavigate the panel to re-join the rearing object. This phase was needed to acquaint the animals with the arena and how to circumnavigate the panel to find the imprinting object. To this aim, the chick was placed in the arena and free to explore for a few minutes with the imprinting object (moved from above the arena via transparent threads). The chick was then inserted in the starting box and presented with the imprinting object moving behind the panel. Once released (i.e., by removing the glass partition), the chick was let free to enter the arena and re-join the object behind the panel. If the chick circumnavigated the panel, the trial was ended, and the chick could spend a few seconds with the imprinting object as a social reward. Training was considered complete when the subject promptly re-joined the imprinting object for three consecutive trials.

2.5. Test

The test was run in the same experimental room and arena as for training, the only difference being the presence of two opaque panels, equidistant from the chick's starting point (approximately 30 cm) and from the centre of the arena (approximately 15 cm), one on the left and one on the right of the chick's starting position (**Fig. 11B**). The testing consisted of 20 consecutive trials and lasted approximately 40 min. While being restrained in the starting box, the chick could see each of the imprinting objects being hidden behind the panel, in a one-by-one presentation. Three objects (i.e., 1 + 1 + 1) were hidden behind one of the panels, and four objects were hidden behind the other one (i.e., 1 + 1 + 1 + 1). The spatial positions of the larger set and the set shown first were counterbalanced between trials.

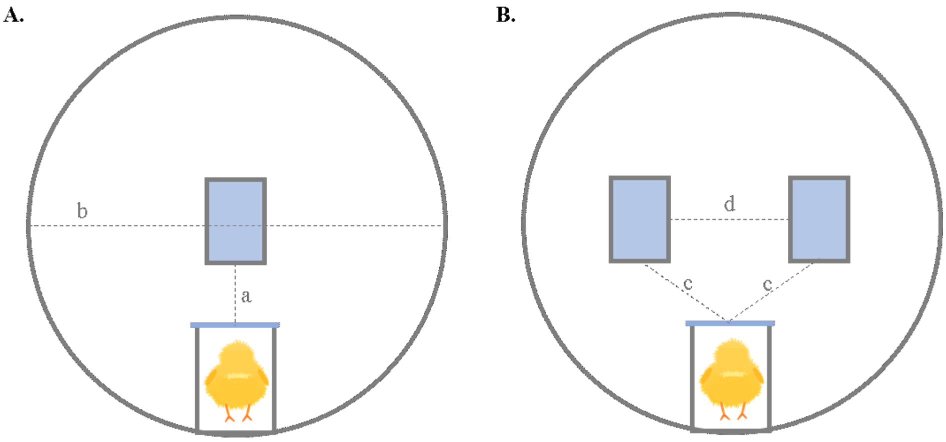


Fig. 11 The experimental arena: A. The setting for training. Only one panel was placed in front of the starting box at a distance of approximately 25 cm (a). The diameter of the arena was approximately 95 cm (b). **B.** The setting for testing. Two panels were present in the arena, approximately 30 cm from the starting box (c) and from each other (d), so that they were equidistant from the chick's starting position; one was on the chick's left and one was on its right.

2.6. Data analysis

In terms of their overall performance during testing, the chicks succeeded in the 3 vs 4 discrimination in Cond. 1 and Cond. 3, whereas they failed and approached both sets at the chance level in Cond. 2 and Cond. 4[115]. The present work aimed to investigate whether chicks perform better when the target set (i.e., the larger) is located on the right side, as in this case they might benefit from the congruency between multimodal information (i.e., spatial and numerical), according to hypothesized left-to-right oriented mental number line. Crucially, for the SNA effect to emerge, the chicks must in the first place be capable of discriminating between the two sets (i.e., Cond. 1 and Cond. 3). Cond. 2 and Cond. 4 were still included in the statistical analysis. In fact, it is possible that the chicks truly failed at discriminating between the two sets (hence, always choosing at random); on the other hand, they might have relied on the SNA and succeeded in the congruent trials only, the results of which could have been lost when looking at the general performance (worsened by the chicks' poor performance in the incongruent trials). This would be in line with what has been reported for the 5 vs 10 and 6 vs 9 comparisons, where chicks showed a facilitation effect even when failing at the overall discrimination (i.e., when elements were controlled for quantitative information)[107]. For these reasons, all conditions were included in the analysis, regardless of the chicks' general performance. However, the results from Cond. 1 and Cond. 3 must be interpreted with caution, as it is possible that the chicks did not show the SNA facilitation because of the impossibility of discerning between the two numerosities in the first place.

Statistical analyses were carried out in R, version 3.6.2[66]. The chicks' responses were coded as a binomial variable (i.e., 0 = choice of the smaller set, 1 = choice of the larger set). As there were multiple observations for each subject (i.e., each chick completed a 20-trial test), a generalized linear mixed model (using the R package lme4[67]) with the subjects as random effects was run to test for the effect of the spatial position of the target set (i.e., left or right) on the chicks' performance. The goodness of fit was tested using the R package DHARMa[88]. The post hoc analysis to test for the direction of the effect was run with the package emmeans[68]. Graphs were generated using ggplot2[69].

3. Results

In all conditions but Cond. 2, the chicks appeared capable of successfully locating the larger set when it was presented on the right side but not when it was on the left one (**Fig. 11**).

In Cond. 2, the chicks behaved at the chance level regardless of the spatial position of the larger set, larger set on the left side: P(choose the larger set) = 0.52, $SE = 0.044$, $z = 0.459$, $p = 0.647$; larger set on the right side: P(choose the larger set) = 0.493, $SE = 0.044$, $z = -0.154$, $p = 0.878$, with no difference between the two conditions (left/right = 1.11, $SE = 0.26$, $z = 0.465$, $p = 0.642$).

In Cond. 1 and Cond. 3, the chicks succeeded when the larger set was on the right side, Cond. 1: *P*(choose the larger set) = 0.636, *SE* = 0.041, $z = 3.17$, $p = 0.002$; Cond. 3: *P*(choose the larger set) = 0.599, *SE* = 0.045, $z = 2.167$, $p = 0.03$, but failed when it was on the left side, Cond. 1: *P*(choose the larger set) = 0.557, *SE* = 0.042, $z = 1.349$, $p = 0.177$; Cond. 3: *P*(choose the larger set) = 0.572, *SE* = 0.045, = 1.572, $p = 0.116$, despite no statistical difference being found between the right and left trials (Cond. 1: left/right = 0.721, *SE* = 0.176, $z = -1.338$; $p = 0.181$; Cond. 3: left/right = 0.893, *SE* = 0.212, $z = -0.475$, $p = 0.635$.

In Cond. 4, the chicks succeeded in the 3 vs 4 comparison when the larger set was on the right side, *P*(choose the larger set) = 0.64, *SE* = 0.039, $z = 3.382$, $p < 0.001$, but not when it was on the left side *P*(choose the larger set) = 0.433, *SE* = 0.041, $z = -1.628$, $p = 0.104$, with the two performances also being statistically different (left/right = 0.43, *SE* = 0.102, $z = -3.562$, $p < 0.001$).

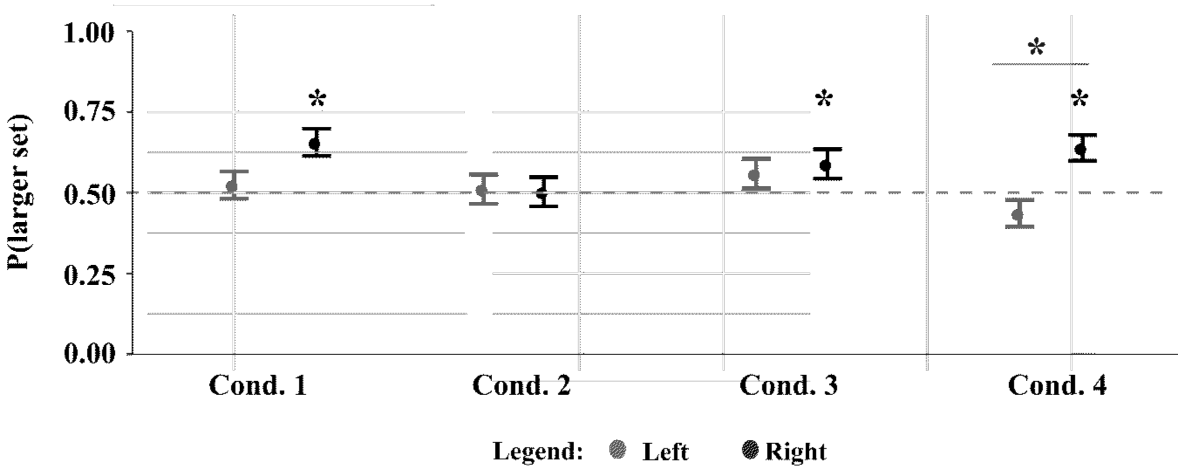


Fig. 11: The chicks' performance depending on the spatial position (left or right) of the larger set. The y-axis shows the probability of the chicks choosing the larger set (i.e., that of four elements). The x-axis shows the four experimental conditions. For each condition, the chicks' performance on the left side is represented in grey, and the chicks' performance on the right side is represented in black. The light grey dashed line represents the chance level (y = 0.5). The asterisks indicate statistically significant results.

4. Discussion

This study aimed to investigating a facilitation effect due to congruency between multimodal information (i.e., spatial and numerical) according to a left-to-right oriented mental number line. In particular, the use of a complex numerical discrimination (i.e., 3 vs 4) made it possible to test whether such a facilitation is affected by the cognitive effort required by the task or whether it relies on a spontaneous low-cognition demanding mechanism that needs no or little resources from the chick. The results support the latter hypothesis, showing that even when facing a task that implies a cognitive overload, the chicks benefitted from congruency between the spatial and numerical information, succeeding at locating the larger set when it was placed on the right side (except for Cond. 2, as discussed later). In fact, relying on the SNA effect could represent a low-cognition-level mechanism that supports discrimination by stressing the redundancy in multimodal information. Indeed, animals often benefit from the compresence of multimodal information, especially during the first stages of development or when they need to represent complex, salient (e.g., social) stimuli (see Discussion in **Study 2** on crossmodal integration). In Cond. 1 and Cond. 3, despite the chicks succeeding only in the right-displacement trials, there was no difference in their performance depending on the left/right presentation side. Conversely, in Cond. 4, such trials appeared to be statistically different. It is worth noting that regarding the chicks' overall performance in Cond. 4, they behaved at the chance level. Hence, this might be the case of the chicks seeming to fail at discriminating when merging their performance in both congruent and incongruent trials, despite them being capable of solving the comparison at least in the congruent trials (i.e., when discrimination is further supported by the SNA facilitation). This is in line with what has been reported for the 5 vs 10 and 6 vs 9 comparisons, where the chicks succeeded during testing in the congruent trials only, while failing in both the incongruent trials and at the overall discrimination[107]. Interestingly, in their study the authors also showed that the resulting facilitation effect was more pronounced compared to that reported for the control conditions (i.e., where the chicks also had access to quantitative information and succeeded in discriminating in the 5 vs 10 and 6 vs 9 comparisons). A possible explanation could be that the chicks that could not solve the task (as in the case of the original study by Rugani et al.[107], and in Cond. 4 of the present study), further stressing the multimodal processing of the stimuli, as the compresence of both spatial and numerical information could boost their performance and allow them to locate the target set at least in half of the trials. This would be in line with a previous work on cognitive flexibility in chicks which showed that chicks sharpen spatial biases and rely on them to increase their probability of success in response to unexpected environmental changes[117].

In Cond. 2, however, the chicks failed at discriminating in the 3 vs 4 comparison regardless of the congruency/incongruence of the SNA. According to the original study, Cond. 2 was designed as a control condition in which, despite the presence of face-like stimuli, individual object processing was never possible (all the stimuli used for rearing and training and testing were identical copies of the same stimulus). Thus, Cond. 2 mirrored the classic 3 vs 4 comparison with all identical stimuli, which chicks have been repeatedly shown to fail[40,89]. If this was the case, the chicks' failure might be the consequence of the discrimination being too difficult, to the point that they were unable to track each element of both sets and represent the resulting numerosities in a dedicated memory engram. Hence, no preference emerged for either set. Whenever individual discrimination was possible (Cond. 1, Cond. 3, and Cond. 4), the chicks could instead complete such an initial processing, representing two sets in their working memory, to eventually compare them and locate the larger one. This latter stage could further benefit from redundancy between the spatial and numerical information, as the chicks' performance is better when the larger set is congruent with the SNA. This implies that even though SNA supports numerical discrimination, such a facilitation takes place only when both sets have been processed and stored in a dedicated mental representation. It is ineffective in the initial stages of stimuli processing, when chicks have to represent each element of the set and add it to the subsequent one up to the final numerosity. This is not unexpected, considering that during the proto-arithmetical task, the chicks saw only one element at a time; thus, they had no information regarding the numerousness of the set. At this stage of processing, different strategies are required, such as individual processing (note that when this was prevented, the chicks failed, Cond. 2). Future studies should be dedicated to testing whether providing numerical information at stimuli presentation (e.g., by means of a grouping strategy) could trigger an early emergence of the space–number associative process.

SECTION 2 – SELECTION OF INFORMATION FROM DIFFERENT SENSORY MODALITIES

Animals acquire, process, store, and remember a large amount of information coming from all sensory modalities and use it to face novel situations and solve problems[118,119]. Each of these mechanisms might be the result of a specialized adaptation that evolved to answer to certain environmental requests and evolutionary pressures[118–120]. In some cases (as shown in **Section 1**), animals benefit from redundancy in information sources because it amplifies the signal, allowing for better detection and faster and more accurate responses. Multimodal stimulation is even necessary to solve certain tasks[46,47], as in the case of the multimodal conditional rule showed in **Study 1**. However, multimodal stimulations might also conflict with one another. This is not unusual in nature because each sensory channel is characterized by a specific spatial and temporal range, and multimodal sensory cues could increase or decrease, depending on several factors external to the individual. Similarly, in complex environments, the predictive power of some information could change over time, thus requiring the animals to exploit different sensory information, selected in response to different situations, rather than one integrated representation. For instance, two possible strategies can be implemented for orienting in space, one based on the arrangement of surfaces defining an enclosed space (geometric information) and another based on discrete elements located inside or outside such a space (landmarks)[71,121–123]. For instance, chicks proved capable of retrieving a food reward hidden in the centre of an arena[124,125] given a beacon (landmark). When the beacon was either removed of shifted to a different location in a test, the chicks were still able to solve the task and locate the centre of the arena by relying on solely geometrical information (despite it not being essential to localise the goal during training), thus inhibiting the processing of landmark-based information (which would instead be deceiving). The capability to select one processing strategy from a wider repertoire of behavioural and cognitive mechanisms allows animals to respond better to novel and/or unexpected environmental requests. In some cases, multiple strategies could serve the same goal, and animals must select the optimal one based on their current needs (e.g., the fastest, the least cognitive demanding, or the most effective). Alternatively, a certain situation could trigger two or more competing alternative responses, each leading to a different outcome. For instance, studies on food caching (i.e., storing food for later consumption) showed how animals could select the optimal caching strategy for the different situations they face. When observed by a potential pilferer, jays re-cached more often, hid their food in more distant sites to reduce visual information, or created fake caches, which could supposedly weigh on the observer's visual spatial memory[126,127]. However, when the observer's view was blocked (e.g., the bird was behind a wall), jays adopted an acoustic-based strategy, hiding food in a (silent) sandy substrate rather than in (noisy) gravel [128], and they did not allocate resources to controlling for visual information (e.g., they did not create fake caches or cache food in distant locations). Interestingly, these were flexible strategies that the animals acquired through experience, as they were implemented only by birds that had experienced at least to one pilfering experience[126–128]. Similarly, squirrels employ evasive tactics during caching only in the presence of potential (conspecific) pilferers but not in the presence of other animals that are not usual pilferers (heterospecific)[129]. A cognitive or behavioural strategy (e.g., which information to process, which perceptual mechanism to activate, or which stimulus characteristics to exploit) is selected through the interplay among available strategies and cognitive capabilities (including inborn predispositions and the results of experiences) and the environment. In the example of food-caching birds, jays must possess some cognitive capabilities, e.g., a long-term memory of a previous experience of pilfering, or a representation of the pilferer's viewpoint (e.g., whether it can hear or see the caching). However, the environment plays a key role as well, allowing the birds to exploit these cognitive capabilities (e.g., there must be a silent substrate in which to hide the food, in the case of acoustic strategies, or an environment wide enough to create multiple fake caches, in the case of visual strategies). The goal of **Study 4** is to test whether newborn chicks could successfully select the relevant information, in the presence of a multimodal stimulation, to solve a complex task. In particular, this study aims to test for the presence of a non-mathematical perceptual strategy to solve a numerical discrimination task. In fact, the experimental stimuli (i.e., sets of elements of different numerosities) could allow for either numerical or perceptual processing. However, while number-based strategies would unlikely be successful (due to the large numerosity of the groups and the high ratio of the employed discriminations), a perceptual mechanism instead could help chicks to solve the discrimination tests (i.e., 7 vs 9, 9 vs 11, and 13 vs 15). The chicks were tested on the day of hatching, after a brief habituation to the visual characteristics (i.e., colour and shape) but not to the numerosity (i.e., all habituation stimuli were of even numerosities, i.e., 4, 6, 10, and 12, whereas odd numerosities were employed during the tests) of the stimuli, to explore whether their early cognitive abilities and predispositions could suffice in enabling them to select the most appropriate strategy with which to analyse the stimuli and correctly respond to the task.

While **Study 4** employed very complex discriminations, to further trigger a perceptual analysis of the stimuli, the chicks in **Study 5** were confronted with a 5 vs 9 comparison, which is relatively easy to solve[101]. Two groups of chicks were presented with a 5 vs 9 comparison. The first group underwent an imprinting procedure, which is known to motivate chicks to re-join the larger group of familiar objects (hence prompting a number-based strategy). The second group underwent a habituation procedure on heterogeneous stimuli, as used in **Study 4**, to trigger a novelty-exploration response (thus prompting perceptual analysis)[130]. The goal was to test whether chicks could select either a number-based or perceptual-based strategy based on their internal objective (i.e., to re-join the larger set or detect novel perceptual patterns, respectively). If the chicks' behaviour differed between the two groups, this would indicate that the two strategies are not selected based the complexity of the discrimination but rather that they are both equally available and selected on the basis of different task requests. Employing the most appropriate strategy (i.e., prioritizing a number-based or perceptual analysis of the stimuli) relies on a conjunct representation of the chicks' previous experience (i.e., imprinting vs habituation) and internal motivation (i.e., seeking the larger set vs detecting novelty).

STUDY 4 – Newly hatched chicks rely on a perceptual mechanism based on symmetry detection to solve complex numerical discriminations

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1. Introduction

Study 3 showed how numerical discrimination could be supported by a multimodal representation of non-numerical (i.e., spatial) and numerical information. People often implement non-mathematical strategies to boost performance in numerical tasks, as in the case of perceptual grouping[131,132]. This mechanism consists of disassembling a certain numerosity into smaller subgroups to favour a multiplicative strategy (that is, multiplying the number of elements in each subgroup by the number of subgroups, rather than adding each element of the set one by one). For this strategy to be effective, however, all subgroups must have the same numerosity (e.g., 9 = 3 + 3 + 3, 12 = 4 + 4 + 4, or 3 + 3 + 3 + 3, etc.) – namely, symmetrical grouping[131]. Such a strategy can be initiated actively by the subject, or passively induced by presenting elements as already grouped (i.e., by colour or by spatial position)[131]. Whenever it is possible to rely on symmetrical grouping, humans show a facility for enumeration tasks, in terms of both accuracy and reaction times[131,132]. However, subjects' performance worsens (reduced accuracy and increased reaction times) when symmetrical grouping is prevented. This can be the case when the stimuli are presented asymmetrically (e.g., a set of 10 elements already grouped as 5 + 3 + 2) or in the case of numerosities that, because of their natural properties, never allow for symmetrical grouping, such as for prime numbers. **Study 4** investigated whether newborn chicks could spontaneously rely on such a non-mathematical perceptual strategy to solve a complex numerical comparison between two sets of elements: one that could not be divided into equally sized subsets (i.e., a prime number) and one that did allow for symmetrical grouping. This would provide evidence of non-numerical perceptual processing of information, which could be implemented to solve a numerical task. Domestic chicks seem to be to the most suitable model for this kind of study. They are widely studied in the field of numerical cognition (see **Study 3** on space-number congruency facilitation effect) and can process object symmetry[36,133,134], rely on Gestalt principles[16], and benefit from induced grouping in a proto-arithmetical task[89].

To test for the presence of a spontaneous grouping mechanism based on symmetry/asymmetry, newborn chicks were first habituated to sets of elements, all with even numerosities (i.e., four, six, 10, and 12). After 1 h of exposition, the chicks were tested in either the 7 vs 9 or 9 vs 11 comparison (Exp.1), with the experimental hypothesis being that if they could implement the symmetrical grouping strategy, they could detect the difference between the two compared sets (i.e., seven and 11 never allow for symmetrical grouping, whereas nine does). As the chicks were habituated to the experimental arena and stimuli (sets of all even numerosities, which allowed for symmetrical grouping), a preference for exploring the novel stimulus was to be expected, i.e., longer exploration time for a set with a prime numerosity, regardless of it being the largest or the smallest of the set. Exp. 2 and Exp. 3 were designed to test for a processing limit in the grouping strategy, by employing an even more complex discrimination task (i.e., 13 vs 15), either with no induced grouping (Exp. 2) or with elements already grouped by colour (Exp. 3). Numerical cognition studies usually employ comparisons between much smaller quantities, e.g., 1 vs 2, 1 vs 3, or 2 vs 3[39,101], or with a much smaller ratio between the two sets, e.g., 5 vs 10[101], 10 vs 20, or 20 vs 40[135] (see Introduction of **Study 3** for a more detailed explanation on numerical ration and processing of numerical information). In all of the comparisons employed in the present study, chicks were presented with large numerosities and high ratio values (0.78 and 0.82 in 7 vs 9 and 9 vs 11, respectively, and 0.87 in 13 vs 15). Birds are unlikely to solve these comparisons by relying on a numerical processing of the sets, which could further support the emergence of perceptual non-mathematical mechanisms such as symmetrical grouping.

2. Materials and methods

2.1. Subjects

A total of 158 (86♀) domestic chicks (*Gallus gallus)* were tested in the study. Fertilized eggs were provided by a local hatchery (Incubatoio La Pellegrina, San Pietro in Gu, PD, IT) and were incubated in the laboratory at controlled temperature (37.5 °C) and humidity (55–66%) and hatched with no light sources (i.e., the chicks were hatched in the dark). After hatching, the chicks underwent the habituation procedure. At the end of habituation, the chicks were left for 1 h in the rearing room, individually housed in standard metal cages (same as described in **Section 1**). After 1 h, they underwent a free-choice test between a prime and an odd non-prime numerosity.

2.2. Habituation

The habituation procedure was the same for all experiments and lasted 1 h. Each chick was placed in a triangular arena (93 × 62 × 30 cm), with one side (i.e., opposite from the vertex in which the chick was placed) being a monitor (Samsung FHD, 24”, 60 Hz) onto which the stimuli were projected (**Fig. 12A**). During this phase, each chick was shown a random sequence of sets of different elements, with each set being presented on the monitor for 10 sec and immediately followed by the subsequent one (**Fig. 12B**). All sets were of an even numerosity (i.e., 4, 6 10, or 12). The elements of each set always had the same shape (i.e., triangle, rectangle, or circle). In Exp. 1 and Exp. 2 (**Fig. 12C**), the elements within each set also were the same colour (i.e., red, blue, green, or yellow). In Exp. 3, elements within each set had the same shape but differed in colour, so that all four colours were shown together in each set. Importantly, two elements of the same colour were never displayed in spatial proximity (**Fig. 12D**). This was necessary to familiarize the chicks with a set having more than one colour, without exposing them to colour grouping prior to the test. All elements of a set were positioned pseudo-randomly (i.e., the elements never overlapped) within a white square area (336 px) in the centre of the screen. Each element covered a total area of 36 px.

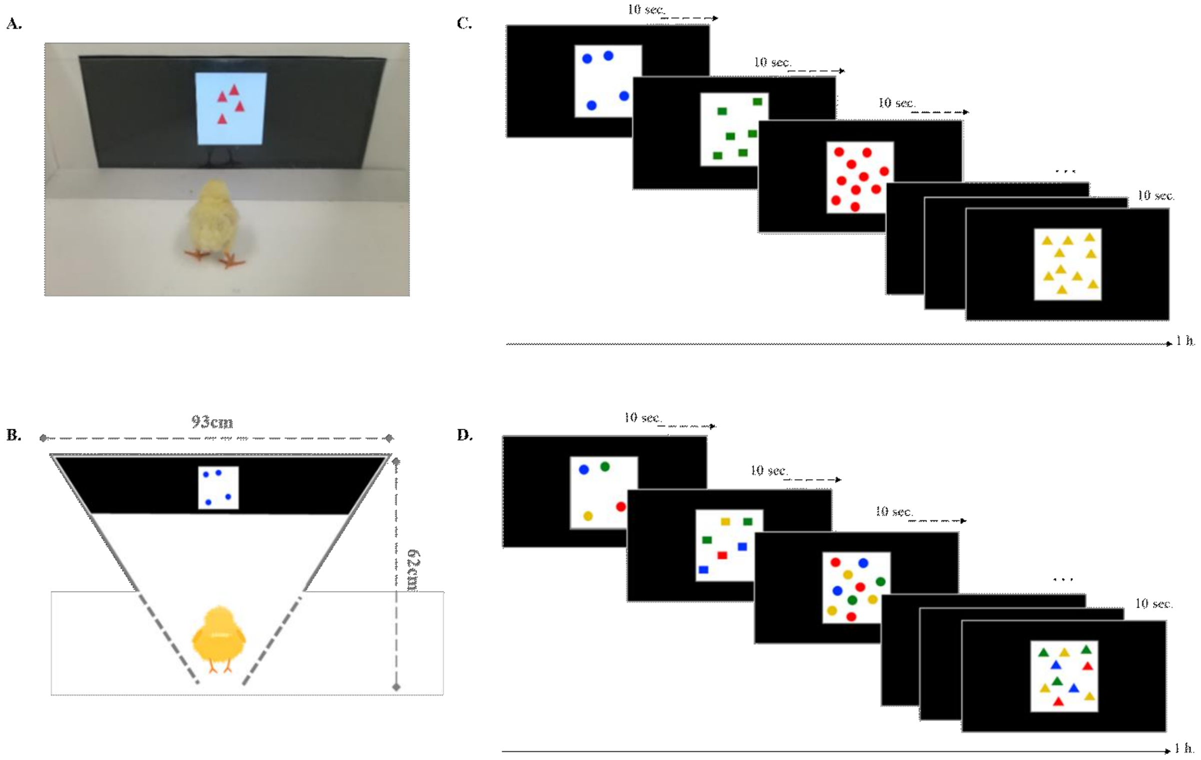

Fig. 12 Habituation arena and stimuli: A. The chick in front of the monitor inspecting one of the habituation stimuli; **B.** The experimental arena. At the beginning of habituation, the chick is placed in the vertex opposite to the monitor and then let free to explore the arena for 1 h; **C.** The habituation paradigm for Exp. 1 and Exp. 2: each stimulus comprised elements of the same colour and shape. It was displayed on the monitor for 10 sec and immediately followed by the subsequent one. The numerosity (i.e., 4, 6, 10, or 12), shape (i.e., triangle, rectangle, or circle), and colour (i.e., red, green, yellow, blue) of each set was determined randomly for each chick. **D.** The habituation paradigm for Exp. 2: each stimulus comprised elements of the same shape but of different colours, with elements of the same colour never been close to each other. The numerosity (i.e., 4, 6, 10, or 12) and the shape (i.e., triangle, rectangle, or circle) of each set was determined randomly for each chick, but all four colours were presented together in each set.

2.3. Test

Upon hatching, the subjects were randomly assigned to one experiment (and experimental condition, in the case of Exp. 1). In Exp. 1, the chicks were tested with either the 7 vs 9 (n = 40, 19♀) or the 9 vs 11 (n = 39, 21♀) comparison. In Exp. 2 (n = 39, 27♀) chicks were tested with the 13 vs 15 comparison, in the absence of any induced grouping strategy. In Exp. 3 (n = 40, 19♀), chicks were tested with a 13 vs 15 comparison (the same as in Exp. 2) with elements already presented grouped by colour. The testing procedure remained the same for all of the experiments. The experimental arena and the experimental room were the same ones used for habitation, with the only difference being that the monitor was divided into two separate halves by a vertical plastic partition (5 cm × 30 cm). Two sets of stimuli were presented at once, one in each half of the monitor (**Fig. 13A**). One set was of a prime numerosity (i.e., not allowing for symmetrical grouping) and one was an odd non-prime numerosity (i.e., allowing for symmetrical grouping). The position of the prime numerosity (left or right) was counterbalanced between subjects. Each pair for the set remained visible on the monitor for 10 sec and was immediately followed by the subsequent pair for the entire duration of the test (5 min). In Exp. 1 and Exp. 2 (**Fig. 13B**), elements of both sets had the same shape and colour (the same as those used for habituation). In Exp. 3 (**Fig. 13C**), they had the same shape, but the elements in each set were grouped by colour (i.e., 5 + 5 + 5 vs 5 + 5 + 3).

Whenever the chick passed the vertical partition, thus entering an area close to one set (from where it could not see the other one), it was considered a preference by the chick for inspecting that set. A camera (Canon Legria HF R606) was placed about 30 cm above the arena, which allowed for offline scoring of the time spent by the chick in each of the two chosen areas. Offline scoring was conducted using the BORIS software[136]. When the test was completed, the chick was feather sexed. This was not done beforehand, to avoid any risk of influencing the chicks' behaviour as a consequence of handling.

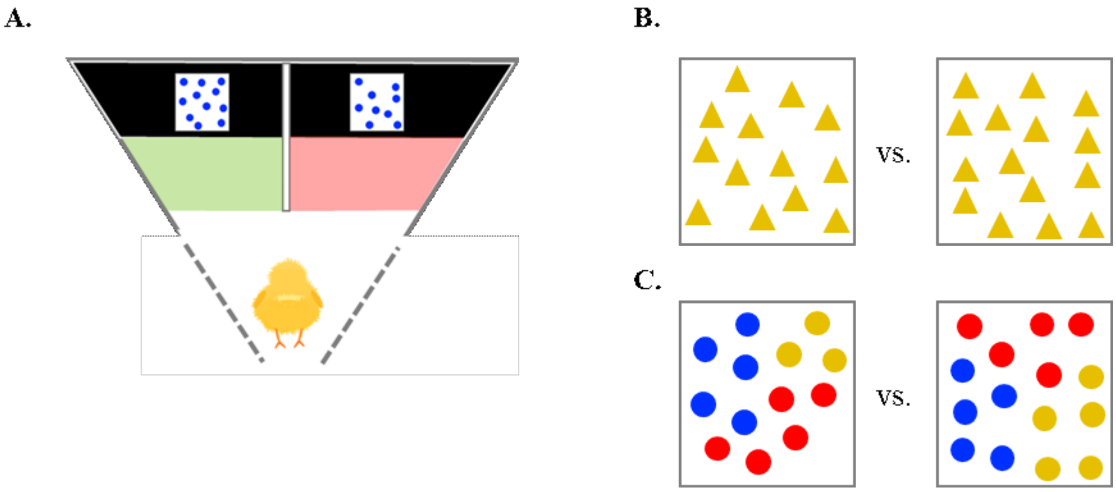

Fig. 13: Test arena and stimuli: A. The testing arena was divided into two separate areas by a vertical partition. A set of elements was presented in each area, with one having a prime numerosity (in this example, 11, in the left half) and the other having an odd non-prime numerosity (in this example, nine, in the right half). The time spent by the chick in each area was scored as being the correct choice for the novel (i.e., not allowing for symmetrical grouping) set and as the incorrect choice for the familiar (i.e., allowing for symmetrical grouping, like the habituation numerosities) set; **B.** An example of a pair of stimuli used for testing without induced colour grouping (Exp. 1 and Exp. 2) – in this case, the 13 vs 15 comparison (Exp. 2); **C.** An example of a pair of stimuli used for testing in Exp. 3, in which the stimuli were presented grouped by colour (13 vs 15 comparison).

2.4. Data analysis

The data were analysed using the R statistical software package, version 4.0.2[66]. A generalized linear mixed model was run with subjects included as a random effect. The dependent variable was the time spent by the chick in each chosen area. In Exp. 1, the independent variables were the stimulus being displayed in the chosen area (i.e., whether it allowed for symmetrical grouping or not), the numerical magnitude (i.e., if it was the smallest or largest in the comparison), the chick's sex (male or female), and the interaction between these factors. In Exp. 2 and Exp. 3, the independent variables included in the model were the stimulus being displayed in the chosen area (i.e., whether it allowed for symmetrical grouping or not), the sex (male or female), and their interaction. The goodness of the fit was checked using the R package DHARMa[88]. A post-hoc analysis with Bonferroni correction (using the R package emmeans[68]) was run to test the direction of the resulting predictors.

A second analysis was run on the chicks' first choice (i.e., which stimulus they approached first at the beginning of the test). This variable was scored as dichotomous (i.e., 0 = the incorrect stimulus; 1 = the correct stimulus); therefore, a generalized linear mixed effect model with a binomial structure was used. The independent variables were the same as those included in the main analysis. All of the graphs were generated using ggplot2[69].

3. Results

In Exp. 1 (**Fig. 14A**), the chicks were tested with either the 7 vs 9 (n = 40) or the 9 vs 11 (n = 39) comparison. An effect of the set numerosity was found (GLMM analysis of deviance, $X^2 = 6.49$; $p = 0.011$), in that the chicks spent longer on prime (i.e., seven or 11) than on composite (i.e., nine) numerosity (post-hoc analysis, *est.* = −30.8; I = 1 1.8; $t = -2.616$; $p = 0.01$). The tested comparison had no effect (i.e., 7 vs 9 or 9 vs 11, $X^2 = 0.797$, $p = 0.372$), nor did its interaction with the stimulus ($\chi^2 = 0.234$, p = 0.629), which suggests no difference between the two conditions, neither in terms of the average time spent in the chosen area (effect of the stimulus) nor in the direction of the preference (stimulus * condition interaction). Similarly, no gender effect was found ($\chi^2 = 0.119$, p = 0.73), which indicates that males and females behaved approximately in the same manner.

The analysis of the first stimulus approached by the chicks at the beginning of the test revealed no preference, $P(1) = 0.557$, $SE = 0.056$, $z = 1.004$, $p = 0.351$.

In Exp. 2 (**Fig. 14B**), the chicks (n = 39) were presented with the 13 vs 15 comparison, to test whether their performance would be affected by the comparison being more complex. As expected, the chicks failed to discriminate between the two sets, and they behaved at chance level, when considering both the total duration of the test (post-hoc analysis, $est. = 31.6$, $SE = 22.4$, $t = 1.412$, $p = 0.162$) and the first approach (post-hoc analysis, $P(1) = 0.475$, $SE = 0.079$, $z = -0.316$, $p = 0.752$). As for Exp. 1, no gender effect was found ($\chi^2 = 0.022$, $p = 0.881$)

In Exp. 3 (**Fig. 14C**), the chicks ($n = 40$) were presented with the same 13 vs 15 comparison as used for Exp. 2, with the only difference being that the elements were already presented grouped by colour (i.e., 5 + 5 + 3 vs 5 + 5 + 5). Under this condition, the chicks' performance was restored, and they could successfully discriminate between the two sets ($X^2 = 14.118$, $p < 0.0001$), showing a preference for the set of 13 elements (post-hoc analysis, $est. = -83.5$, $SE = 22.5$, $t = -3.707$, $p < 0.001$). In line with the previous experiments, there was no difference between male and female chicks ($\chi^2 = 0.146$, $p = 0.703$). However, interestingly, in this case the preference for the prime numerosity was already visible also when analysing the chicks' first choice (post-hoc analysis, $P(1) = 0.706$, $SE = 0.078$, $z = 2.326$, $p = 0.02$).

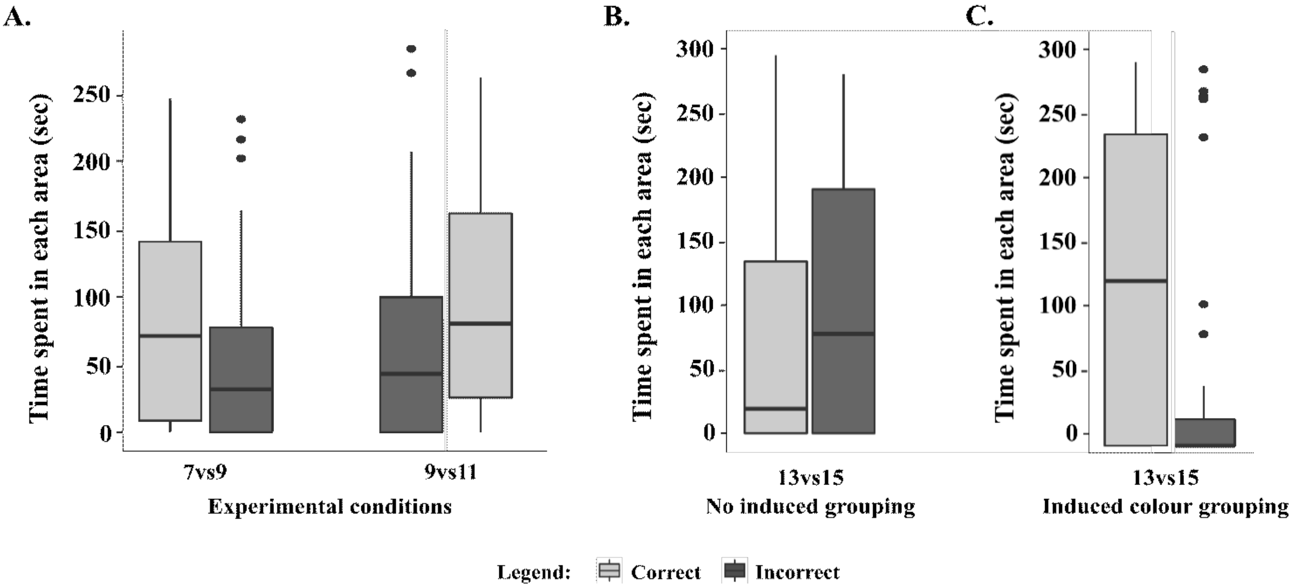

Fig. 14 Time spent near each set of the comparison (on the y axis, in sec): A. Results from Exp. 1. The chicks spent longer in areas close to the set with prime numerosity (in light grey), regardless of it being the smaller (i.e., 7 vs 9, on the left) or the larger (i.e., 9 vs 11, on the right) of the comparison; **B.** Results from Exp. 2. The chicks behaved at chance level, approaching both sets equally in the 13 vs 15 comparison. In Exp. 2, no passively induced grouping was

provided, and the elements all had the same colour and shape, and were randomly dispersed in space (as with Exp. 1); **C.** Results from Exp. 3. The chicks showed a preference for the set with 13 elements (i.e., the one with a prime numerosity, as represented in light grey). Under this condition, elements of each set were presented grouped by colour (i.e., 5 + 5 + 3 vs 5 + 5 + 5).

4. Discussion

The present work involved testing whether newborn chicks could rely on a non-mathematical strategy based on detecting perceptual symmetry to solve complex numerical discrimination tasks. In Exp. 1, two groups of chicks were presented with the 7 vs 9 or the 9 vs 11 comparison. In both cases, the chicks could discriminate between the two sets, inspecting the one with a prime numerosity for longer (i.e., the one that did not allow for symmetrical grouping), regardless of it being the smallest or the largest in the comparison. The chicks were unlikely to have relied on numerical strategies because both tests involved large numerosities and ratios, making the comparison very hard for the chicks to solve[19,39,101]. In addition, a number-based strategy could not explain the direction of the choice because the chicks preferred the smaller set in the 7 vs 9 comparison and the larger set in the 9 vs 11 comparison. Conversely, such behaviour could be explained by referring to a perceptual mechanism. The chicks were first habituated to sets of even numerosities, i.e., those allowing for symmetrical grouping. Then, the chicks were presented with two sets, both of a novel odd numerosity: one set still allowed for symmetrical grouping (i.e., with nine elements), whereas the other one did not (i.e., with seven or 11 elements). If chicks were processing the set by disassembling them into smaller subsets and prioritizing symmetrical patterns, whenever possible [133,134] (i.e., all subsets having the same number of elements), they should have spotted a perceptual difference in sets with prime numbers (i.e., not allowing for symmetrical grouping). Because the chicks were previously habituated to the testing arena and to the colour and shape of the elements in each set, they were likely to display behaviour oriented toward novelty exploration[37,38].

Consequently, they spent longer inspecting the set they perceived as more novel, with respect to their experiences during habituation, which led to the reported preference for prime numerosities.

Exp. 2 involved testing whether such a perceptual grouping mechanism was affected by limits in working memory and the cognitive effort required for perceptual processing. To achieve this goal, the chicks were tested with the 13 vs 15 comparison. The habituation and test protocol remained identical to Exp. 1. A limit of four maximum "files" represented simultaneously in working memory has been reported for both infants[109,137] and chicks[89]. In the original study on induced grouping as a strategy to improve proto-arithmetic performance, chicks were tested in the critical 3 vs. 4 comparison (see Study 3 for a detailed discussion on the 3 vs. 4 comparison) under to possible conditions. A group of chicks was presented with 1+1+1 vs. 1+1+1+1 objects, each set being hidden one-by-one behind one of two opaque panels. Chicks were not able to solve the discrimination and approached both panels at chance. The experimental group, however, was presented with elements already grouped as 2+1 vs. 2+2. This kind of presentation was hypothesised to have some beneficial effect on the performance by reducing the load on working memory. In fact, being the items already grouped, they could be represented together in one "file". After this manipulation, chicks' performance was restored, and they successfully located and re-join the larger set.

For the symmetry-based strategy to take place, chicks had to represent and disassemble the two sets of the comparison mentally; therefore, a similar working memory limit might have occurred. This would be the case for the 13 vs 15 comparison, considering both the number of subgroups (e.g., 15 = 3 + 3 + 3 + 3 + 3) and the size of each subgroup (e.g., 15 = 5 + 5 + 5). Consistent with the hypothesis, the chicks failed in the discrimination task and approached both sets at chance level.

Previous studies in 3-day-old chicks showed that passively induced strategies could support performance in numerical discrimination[40,89]. Exp. 3 tested for this possibility, to see whether newborn chicks could in fact benefit from passively induced grouping. The results showed that chicks could discriminate effectively when the elements were presented grouped by colour (5 + 5 + 3 vs 5 + 5 + 5), and, in line with the results from Exp. 1, that they preferred the set displaying asymmetrical grouping. This was also the case when considering only the first approach, which might constitute further evidence of induced grouping facilitating discrimination.

This is a first evidence of such a young animal (the chicks were tested immediately after hatching) solving a very complex numerical discrimination task. Moreover, it seems that baby chicks are already sensitive to passively induced strategies, which can help with overcoming working memory constraints.

STUDY 5 – Task-dependent use of number-based or perceptual-based strategies in baby chicks

Loconsole, M., Tedaldi, E., Regolin, L., Task-dependent use of mathematical vs. perceptual strategies for numerical discrimination in day-old domestic chicks (*Gallus gallus*). *In Preparation.*

1. Introduction

The results from **Study 4** shed light on a non-mathematical perceptual mechanism upon which day-old chicks could rely to solve complex numerical discrimination tasks[130]. Interestingly, no previous evidence existed of numerical abilities in one-day-old chicks (the youngest age at which chicks were tested in previous studies was 3 or 4 days[39,40,89,99]). This opens up the question of whether the baby chicks relied on the reported perceptual mechanism because it was the most suitable to solve the task (i.e., to seek novelty) or whether number-based strategies were not yet available at such a young age. **Study 5** addresses this issue through two experiments, each involving testing a group of chicks in the same 5 vs 9 comparison. Chicks were tested at the same age and in the same experimental arena; however, the two groups differed in the kind of stimuli to which they were exposed and their early post-hatching experiences, which were designed to prompt for either a perceptual or a numerical-based strategy. In particular, Exp. 1 employed the same exposition procedure (i.e., habituation to sets of experimental stimuli and experimental arena) as described for **Study 4** (Exp. 1 and Exp. 2), whereas the chicks in Exp. 2 were individually reared alongside three-dimensional red balls and tested with those stimuli. Previous studies showed that this kind of exposition (i.e., the chicks can physically interact with the stimuli, which oscillate upon contact and are constantly present in the chick's living environment) chicks develop a social attachment (i.e., an imprinting response) to the artificial rearing stimuli. In fact, when tested in a numerical comparison task, they prefer to re-join the larger set of these social companions[39,99]. If both perceptual and numerical-based strategies were equally available to the baby chicks, it could be possible to predict a preference for a smaller but novel (in terms of symmetrical/asymmetrical grouping) set (i.e., with five elements) in Exp. 1 and a preference for the larger set (i.e., with nine elements) in Exp. 2. Contrarily, if chicks at this age could only rely on perceptual symmetry, there should be a preference for the prime numerosity in Exp. 1 (similar to **Study 4**) but no preference for either set in Exp. 2 (i.e., chicks behaving at chance level because they are incapable of solving the discrimination task and locating the larger set). Another possibility might be that the chicks rely on the perceptual strategy in response to the numerical discriminations presented in **Study 4** being too difficult to solve by a mathematical mechanism. **Study 5** also controlled for this eventuality by employing a much easier comparison, i.e., 5 vs 9 (ratio = 0.56). Chicks have already been proven capable of solving numerical discrimination tasks with similar numerosities[101] (e.g., 5 vs 10 and 6 vs 9) and ratios (e.g., 0.5 as in 5 vs 10 or 20 vs 40[135] as well as 0.67 as in 6 vs 9[101]). If the chicks in fact opted for perceptual-based strategies only when they failed number-based ones, then subjects from Exp. 1 should not have displayed the previously reported preference for the set that could only be asymmetrically grouped.

2. Materials and methods

2.1. Subjects

Fertilized eggs were obtained from a local hatchery (Incubatoio La Pellegrina, San Pietro in Gu, Padova, IT) and incubated at controlled temperature (37.5 °C) and humidity (55–66%). Upon hatching, the subjects were randomly assigned to Exp. 1 or Exp. 2. The rearing room and the rearing cages were the same as described in **Section 1**.

2.2. Experiment 1 rearing conditions and habituation

A total of 35 chicks, 26 of which were females, was tested in the study. Based on the data collected in Study 4 there was no reason to hypothesise an effect of gender, thus all chicks were included in the experiment regardless of the sex. Chicks underwent a habituation procedure identical to that described for **Study 4** (**Fig. 15A**). The only difference is that in this study, habituation took place 24 h after hatching. The chicks were hatched and kept at a controlled temperature (29–30 °C) and humidity (55–60%) in a dark environment, in order to prevent visual stimulation prior to habituation. This was required to match the age at which the chicks underwent testing with that of the subjects from Exp. 2 (which required a longer exposure time for the social attachment to take place, see 2.3.).

2.3. Experiment 2 rearing conditions

Upon hatching, the chicks were feather sexed to select females (which are more motivated to respond to social stimuli[87]). A total of 35 subjects were tested. The chicks were reared individually in standard metal cages with a set of seven artificial social stimuli. These were red plastic balls (4 × 3 × 3 cm) suspended at 2–3 cm from the cage floor via a transparent thread. The chicks remained with their imprinting objects for approximately 24 h after hatching and then entered the testing procedure (**Fig. 15B**).

2.4. Test

The tests for Exp. 1 and Exp. 2 were run in the same experimental arena (the same one employed for **Study 4**). In Exp. 1 (**Fig. 15A**), the stimuli were the same as **Study 4**, with the only difference being in the numerosity of the sets (the chicks were presented with the 5 vs 9 comparison). In Exp. 2, the stimuli were the same 3D objects used during rearing. These were hung in each chosen area (in the 5 vs 9 comparison) with a transparent thread (**Fig. 15B**). In both Exp. 1 and Exp. 2, the position of the larger set (left or right) was counterbalanced between subjects.

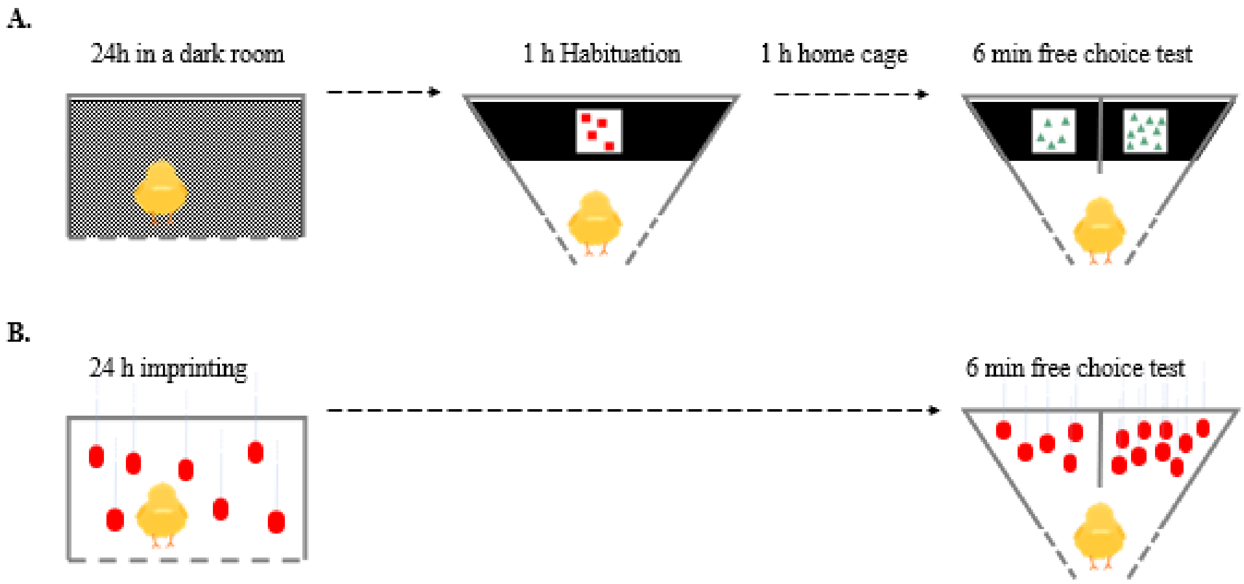

Fig. 15 Experimental procedures: A. Exp. 1. The chicks are kept in darkness for 24 h, at the end of which they underwent a 1-h habituation test (as described in **Study 4** 2.2.). At the end of the habituation, the chicks were placed in a rearing cage for 1 h and then tested with the 5 vs 9 comparison. The testing stimuli were identical to those used for habituation regarding shapes and colours but with a different numerosity. **B.** Exp. 2. The chicks were housed individually along with 3D imprinting stimuli (i.e., red plastic balls). After 24 h, they were tested with the 5 vs 9 comparison. The arena was the same as that used for Exp. 1, and the stimuli composing each set were red plastic balls that were identical to the rearing ones.

2.5. Data analysis

The data were analysed using the R statistical software, version 4.0.2[66]. A generalized linear mixed model was run for each experiment, including subjects as a random effect. The dependent variable was the time the chick spent in each chosen area, whereas the independent variable was the numerosity of the set presented in each area (i.e., five or nine). The goodness of the fit was checked using the R package DHARMa[88]. A post-hoc analysis (using the R package emmeans[68]) was run to test the predictor's direction. All of the graphs were generated using ggplot2[69].

3. Results

Neither the set numerosity ($X^2 = 0.021$, $p = 0.884$) nor the pretest experience ($X^2 = 0.048$, $p = 0.827$) had an effect, whereas the interaction between set numerosity and pretest experience had a significant effect ($X^2 = 9.81$, $p = 0.002$). In Exp. 1 (**Fig. 16A**), the chicks were tested in the 5 vs 9 comparison after habituation to sets of even numerosities (4, 6, 10, and 12) with different colours (red, yellow, blue, and green) and shapes (triangles, rectangles, and circles). This habituation proved effective in prompting a preference among baby chicks to explore slightly novel stimuli, based on a perceptual analysis of the stimuli (**Study 4**). In line with this evidence, chicks in Exp. 1 spent longer by the set of five elements (i.e., the smaller of the compared sets, which did not allow for symmetrical grouping; post-hoc analysis, $est.(5\text{–}9) = 55$; $SE = 26.2$, $t = 2.103$, $p = 0.043$).

In Exp. 2 (**Fig. 16B**), the chicks were reared together with artificial 3D objects. This procedure is known to trigger social attachment to the rearing objects, thus motivating chicks to re-join the larger set of such objects in a comparison[39,99]. The results were in line with previous evidence, in that the chicks spent more time close to the set of nine elements (i.e., the larger of the compared sets, allowing for symmetrical grouping; post-hoc analysis, $est.(5\text{–}9) = -60.4$; $SE = 26$, $t = -2.326$, $p = 0.026$).

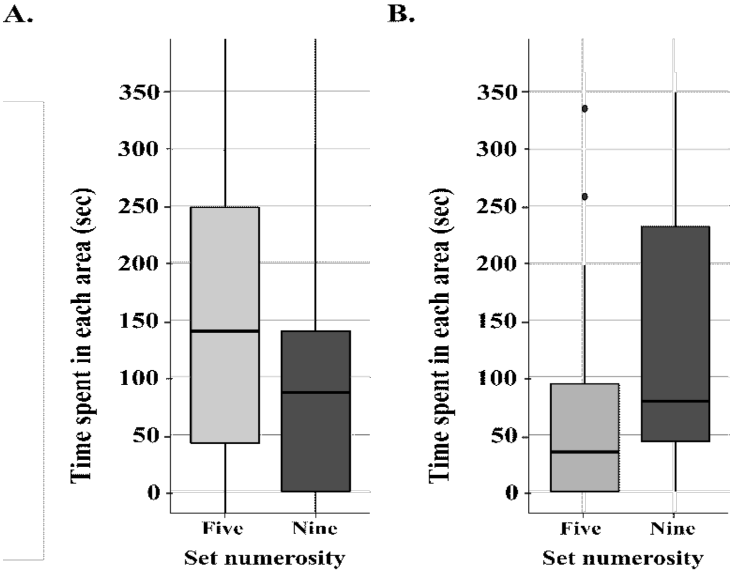

Fig. 16 Time spent close to each set in the comparison (on the y axis, in sec): A. Results from Exp. 1 (Habituation). Under this condition, the chicks spent more time close to the set of five elements (in light grey) in the 5 vs 9 comparison; **B.** Results from Exp. 2. (Imprinting). Under this condition, the chicks spent more time close to the set of nine elements (in dark grey) in the 5 vs 9 comparison.

4. Discussion

In the present work, day-old chicks were tested in a free-choice task with a 5 vs 9 comparison. The first group of chicks underwent a 1 h habituation phase (Exp. 1), during which the subjects were acquainted to the experimental arena and stimuli (sets of elements with different shapes, colours, and numerosities). Such a procedure prompts a preference for exploring slightly novel stimuli[37,38,130]. In the case of Exp. 1, chicks were exposed to sets with an even number of elements (i.e., four, six, 10, or 12), thus all allowing for perceptual symmetrical grouping. Therefore, in the 5 vs 9 comparison, a response to novelty based on perceptual properties would imply a longer exploration time for the set of five elements (i.e., not allowing for symmetrical grouping). A separate group of subjects (Exp. 2) matched for age was reared for 24 h with a set of identical imprinting objects (i.e., red plastic balls) and then tested in the 5 vs 9 comparison. The chicks had never experienced the arena before (because familiarity with the environment further support novelty-seeking behaviours[38]). In addition, they were highly motivated to re-join the larger set of familiar objects because of the imprinting procedure. The results showed that the chicks in Exp. 2 did spend more time close to the set of nine elements.

Overall, these data suggest that day-old chicks are capable of relying on either perceptual or numerical strategies to solve a discrimination task and employ the optimal strategy based on a conjunct representation of their previous experience (i.e., habituation or imprinting) and internal motivation (i.e., exploring the novel set or rejoining the larger set). Importantly, for either strategy to emerge, the chicks also had to possess the cognitive mechanisms required for exploiting the exact perceptual information in each of the two contexts. Thus, the baby chicks need to possess a long-term memory system (**Study 1** also provides evidence of such a mechanism in 4-day-old chicks) because they correctly remembered their pretest experience (either habituation or imprinting) and had a working memory system, with which to represent and mentally manipulate the two sets for the comparison (for the grouping to take place or to compare numerosities). As a precocial species, chicks hatch with fully developed motor and visual systems, enabling them to interact with the environment from the very first moments of life[16,116,138]. However, while early individual–environment interaction has been studied widely in the literature[2,15,16,116], this study provides important evidence that chicks can rely on these early available mechanisms and predispositions to select the optimal strategy among a wider repertoire of possible alternatives. Notably, the strategy selection was not affected by previous learning of that specific mechanism because the chicks were tested within 24 h after hatching, having no experiences other than those from the experimental procedures. This suggests that chicks must be capable of spontaneously analysing their current situation (in all of the aforementioned components of the goal–capabilities–environment interplay) and rely on such an analysis to estimate the best strategy to employ. One can hypothesize that, after gaining more experiences, chicks should be also able to include previous knowledge (e.g., the number of successful vs unsuccessful outcomes resulting from a certain strategy) in the strategy-selection process. Further studies should be dedicated to deepening this possibility, to address the extent to which chicks can rely on their innate or early available capabilities in selecting a strategy and the extent to which experience shapes and possibly improves such a process.

CONCLUSIONS

The aim of this work was to study the roles of predispositions and early available mechanisms on information processing in an avian model, i.e., the domestic chicken (*Gallus gallus*). **Section 1** was dedicated to multimodal information integration. In particular, **Study 1** provided evidence of long-term memory for spontaneously encoding integrated representations of multimodal conditional rules as well as the presence of a system lateralized to the left hemisphere. **Study 2** investigated a peculiar case of spontaneous multimodal integration of non-redundant information, namely crossmodal correspondences, supporting the idea that this precocious mechanism is widespread among different species (at least in the clades of mammals and birds). **Study 3** tested whether spontaneous multimodal integration could sustain processing in a complex cognitive task, acting as a further strategy (external to the experimental requests) to support performance.

Section 2 focused on chicks' capability to select the information-processing modality successfully that would most likely lead to the desired outcome. **Study 4** explored the presence of a non-mathematical perceptual strategy to allow chicks to solve numerical discriminations that are too complex for numerical processing. **Study 5** further deepened the understanding of how such a mechanism functions, clarifying whether it truly reflects an initial strategy-selection process (i.e., perceptual vs numerical) or whether it results from cognitive constraints or limits among the baby chicks (i.e., the chicks were tested 24 h from hatching, when numerical capabilities might not be yet available).

Altogether, these studies show evidence that chicks can select a preferred multimodal or unimodal channel for processing environmental information. This selection is the result of chicks' predispositions and early available cognitive and behavioural capabilities, and it is further modulated by the internal representations of their goals (i.e., established in response to different environmental requests). In other words, chicks do not simply receive sensory information as it is, but rather they process it and mentally manipulate it to create an integrated representation that also takes into account their internal models and expectations about the environment.

The use of naïve animals with a fully controlled after-hatching experience made possible to explore how early such a flexible strategy selection for information processing emerged, pointing to the presence of biological predispositions that might represent the basis for the development of subsequent (more complex and refined) cognitive capabilities. These bear a strong ecological value because they allow efficient processing of the environment, to select components rapidly that are relevant to the task and isolate them from the background noise to create an integrated and exhaustive representation of the surroundings. Overall, chicks proven to be one of the best model for studying early subject–environment interactions because they proved capable of extracting multimodal and unimodal information in several unsupervised (i.e., in the absence of any formal training or experience) situations and could rely on the corresponding mental representations to solve different tasks successfully. This paves the way for further investigation of multimodal processing's adaptive function, to shed further light on the computational abilities used in the wild to process information and respond to fast and unexpected environmental changes.

ETHICAL STATEMENT

All the chicks that participated to the experiments reported in this work were thereafter donated to local farmers regularly registered to the regional agricultural consortium. Donation took place at the end of each week, upon completion of the experimental session. All experiments were conducted in accordance with the ethical guidelines indicated by the European and Italian laws. Study 1 was examined and approved by the Ethical Committee of the University of Padova: Comitato Etico di Ateneo per la Sperimentazione Animale (C.E.A.S.A 07/11 I.C.S.), Prot. 09/2011. Study 2, Study 4 and Study 5 were examined and approved by the Ethical Committee of the University of Padova: Organismo Preposto al Benessere Animale (O.P.B.A) and by the Italian Ministry of Health, Prot: 196/2017-PR. Study 3 was examined and approved by the Ethical Committee of the University of Padova: Organismo Preposto al Benessere Animale (O.P.B.A) and by the Italian Ministry of Health, Prot: 192/2017-PR

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