Short Communication

Evidence for interhemispheric conflict during meta-control in pigeons

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HIGHLIGHTS

- We showed that meta-control is not only a stimulus dependent process.
- We found that different reaction time responses to stimuli involved congruent and incongruent can be indicator of interhemispheric conflict.
- We found that deviations of planned movement trajectory can be another indicator of interhemispheric conflict.

ABSTRACT

In birds each hemisphere receives visual input from the contralateral eye. Since birds have no corpus callosum, avian brains are often seen as 'natural split brains'. How do birds cope with situations, when both hemispheres are brought into conflict? If under such conditions one hemisphere completely determines the response, this is called meta-control. This phenomenon has recently been demonstrated in pigeons. The aim of the current study is to test, if meta-control results from an interhemispheric conflict that would require interhemispheric interaction, possibly via the commissura anterior. To this end, we trained pigeons in a forced-choice color discrimination task under monocular condition such that each hemisphere was trained with a different pair of colors. Subsequently, pigeons were binocularly tested with conflicting and non-conflicting stimulus patterns. Conflicting stimuli indeed produced a delayed reaction time as expected when two divergent decisions create a conflict. In addition, we sometimes observed a pecking pattern that seemed to represent the average of two discrepant and hemisphere-specific movements. Thus, pigeons possibly undergo interhemispheric conflict during meta-control even without a corpus callosum. However, also when having decided to peck a certain color, the planned movement trajectory of the other hemisphere sometimes compromises the final pecking movement.

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When both hemispheres are brought into conflict, often one of them takes charge of the behavioral output. This is known as meta-control and has been repeatedly demonstrated in humans [1–3] and more recently also in monkeys [4], pigeons [5] and chicks [6]. In the last mentioned study, chicks were shown to focus on global features of the environment under binocular condition. This is characteristic for the right hemisphere, while the left hemisphere mostly attends to local features. The first demonstration of meta-control was performed with split-brain patients who were asked to match lateralized and tachistoscopically presented stimuli to other pictures presented in free vision on the basis of either appearance or function [1]. Half of the tachistoscopically delivered stimuli were chimeric composites of two different pictures that were aligned along the vertical meridian. Thus, the two hemispheres were confronted simultaneously with discrepant input. Subjects were asked to match the tachistoscopically presented stimuli to those seen under free vision. According to the instructions, this match had sometimes to be done by function or, in other trials, by appearance. Most importantly, in some trials no instruction was given and subjects were free to employ any matching strategy. Under these ambiguous conditions, appearance and function matches were performed by right and left hemispheres, respectively. Thus, unilateral hemispheric control became visible when subjects decided on their own strategy of choice. In subsequent studies, meta-control effects were also observed in split-brain monkeys [4] and human subjects with intact commissures [2,3]. Moreover, observed meta-control effects seemed to depend on the strategy chosen by the subjects [2] or exposure time of stimuli [3].

The core assumption of all of these studies is that meta-control results from a response conflict between hemispheres. This then results in an outcome in which the perceptual specialization of one hemisphere dominates over that of the other. This inter-hemispheric conflict is assumed to be realized by pathways like the corpus callosum which is known to predominantly

mediate inhibitory effects [7,8]. Surprisingly, the existence of inter-hemispheric response conflict as the explanans of meta-control was, to the best of our knowledge, never tested. If it holds, it should leave characteristic traces at reaction time and response configuration level: usually, conflicting conditions produce longer reaction times than non-conflicting ones [9,10]. This is possibly due to the longer processing time that is required to activate a response when two incompatible options compete with each other [11]. Additionally, when unihemispheric control is not absolute, we would expect that the movement trajectory with which the choice reaction is executed could incorporate a mixture of the different motor plans of the two hemispheres. Because these basic requirements were never tested, we set out to test pigeons under lateralized conditions in a meta-control task in which hemisphere-specific reaction times and movement parameters for conflicting and non-conflicting stimuli could be obtained. For this to do, we had to use a different procedure than Adam & Güntürkün (2009) [5] who had employed a Go–NoGo task. Instead, we used a forced-choice procedure in which the animals always had to respond to all stimuli. Our prediction was that reaction time should be a function of response conflict and thus should be longest in the meta-control trials. In addition, we assumed that their final peck location during critical trials reflects a compromise between the different response options of the two hemispheres.

15 homing pigeons (*Columba livia*) of both sexes, obtained from local breeders were used. They were kept in individual cages on a 12-h/12-h light–dark cycle with the other conspecifics. They were kept at 80–90% of their free feeding weight. Water was available ad libitum. For the monocular experimental sessions, rings of Velcro were fixed to the skin around the pigeons' eyes. Thus the eye caps made by cardboard could be easily attached. The experiment was conducted in a 40 cm × 35 cm × 35 cm (W × D × H) custom made operant chamber, illuminated by a house light and equipped with a feeder. This feeder was also illuminated when the food was released. The stimuli were presented on a TFT LCD touch-screen monitor, with a resolution of 1024 × 768 pixels. The programs for the experimental sessions were controlled by the MATLAB-Biopsy Toolbox [12].

Prior to training, all subjects were autoshaped to peck on a white square in a standard procedure containing 40 trials. The stimulus was presented for 4 s and was followed by food access. After the subjects reliably responded to this white square, they continued with variable ratio (VR) schedules with 40 trials per session and were progressively trained with variable ratios VR2, VR4, and VR8 under monocular conditions. Each schedule continued until the subjects responded the positive stimulus in more than 85% of the trials in two consecutive sessions per eye condition. After that, they started with the color discrimination. Four differently colored rectangular stimuli (red, yellow, green, or blue) were used, which were always together with a white rectangle of identical size. Pigeons were trained under monocular conditions and each eye was trained with a different pair of stimuli (e.g. red and yellow for left eye (LE), blue and green for right eye (RE)). For each eye, one color served as S+ and the other as S−. The sequence of monocular sessions was balanced. As shown in Fig. 1, the pigeons had to choose between an upper and a lower compound stimulus that each consisted of a color and a white rectangle. Pecks on the compound that contained the S+ color were rewarded, regardless if the location of the peck was on the colored or on the white compartment of the compound. This also applied to the S− compound.

The stimuli were presented for 4 s each. Pecking on the positive stimulus compound (S+) activated access to food for 2 s. Pecking on the negative stimulus (S−) resulted in a time out of 5 s with the houselights turned off and a loud noise turned on for 1 s. When subjects responded to the positive stimulus in more than 85% of the trials in two consecutive sessions per eye conditions, the number
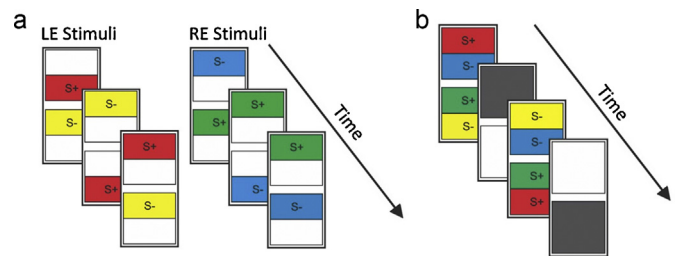
Fig. 1. Schematic depiction of the stimuli and the experimental design in the different test phases. (A) Training stimuli shown during sessions conducted with left eye (LE) or right eye (RE) open. The pigeons could either peck on the upper or on the lower compound. To obtain reward, it was irrelevant whether they pecked the S+ color or the white component of the respective compound. (B) Ambiguous stimuli consisted of two compounds that both contained an S+ of one hemisphere and an S− of the other hemisphere. Super stimuli contained a compound with both S+ colors and another with both S− colors. Ambiguous and super stimuli were run as catch trials. In both ambiguous and super stimuli the peck on the upper or the lower compound was relevant for the outcome; the location of the peck within the compound was not. White/Gray stimuli (the white key was the S+) served as a simple discrimination procedure during test sessions that resulted in reward upon pecking the white key. (For interpretation of the references to color in figure legend, the reader is referred to the web version of the article.)

of trials was successively increased up to 200 in step of 20 trials at each time. In each step, subjects had to perform at least 85% correct choices to the positive stimulus for each eye condition in one session. While the number of trials of sessions was increased, the probability of reward amount was decreased in steps by 10% until 40% reward probability was reached. This was necessary to constitute resistance for extinction during subsequent catch trials. In the last step, each session consisted of 200 trials, 20% of the stimuli of the session were presented as white (S+) and gray (S−) square stimuli while the rest of the stimuli remained as described before. It was necessary to introduce the white/gray "dummy" discrimination to keep the subjects' responses going during the critical test sessions in which the colored stimuli were newly arranged to create "super" and "ambiguous" stimuli which were run as catch trials. Super stimuli resulted from the combination of both S+ (the S+ of one eye and the S+ of the other eye) on one pecking key and both S− on the other key. Since the critical test sessions were conducted under binocular conditions, we expected fast reactions and high accuracy to the super stimuli. The same was expected for the gray/white stimuli since they also represented a common associative background for both stimuli. This was different for the ambiguous stimuli. Here, the S+ of one hemisphere was always combined with the S− of the other hemisphere on each key. Thus, in these catch trials there was no logical choice since each hemisphere should opt for a different response, based on past learning history. We expected that these trials should produce a response conflict and therefore slower reaction times. The number of catch trials were 40 (20% of the trials) with the remaining 160 stimuli (80%) consisting of white/gray stimuli. Catch trials were never reinforced or punished while white/gray stimuli had 40% reward probability. After the first critical test session that included catch trials, subjects were trained again with the well-known training stimuli under monocular condition. This sequence was repeated until enough catch trial responses were collected.

The subjects needed on the average 8.4 sessions until they reached learning criterion during color discrimination learning for both left and right eye conditions. Subsequently, pigeons reached learning criteria with their right eye/left hemisphere on the average 8.4 sessions, with their left eye/right hemisphere on the average 8.5 sessions. There was no significant difference between training time of the two eye conditions ($t (15) = −0.062$, $p = .951$).

In the test sessions conducted under binocular conditions, we did not find an overall significantly higher choice rate for left or