Contents lists available at ScienceDirect

Behavioural Brain Research

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.

ARTICLE INFO

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

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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
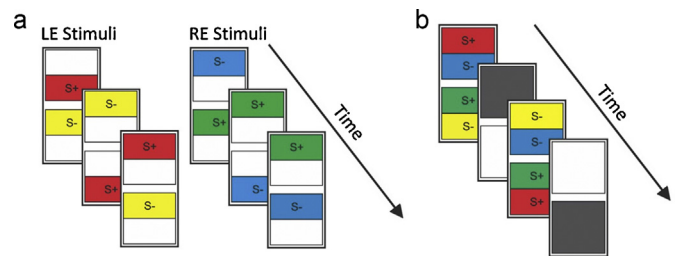

Fig. 1. Schematic depiction of the stimuli and the experimental design in the different test phases. (A) Training stimuli shown during sessions conducted with left eye (LE) or right eye (RE) open. The pigeons could either peck on the upper or on the lower compound. To obtain reward, it was irrelevant 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
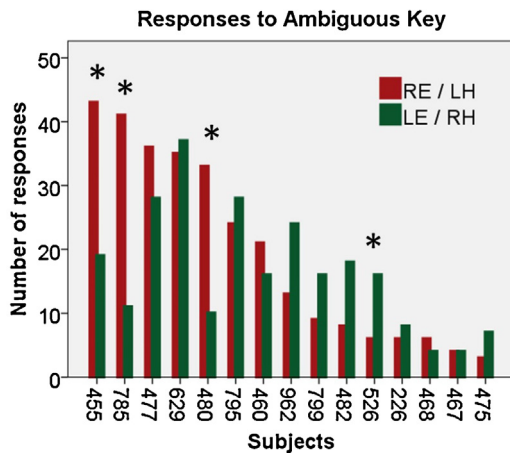
Responses to Ambiguous Key

Fig. 2. Number of responses of the different pigeons to the ambiguous key using the left eye/right hemisphere (LE/RH) or the right eye/left hemisphere (RE/LH). The bars represent how much responses were given during catch trials. Subjects 455, 785, 480, and 526 displayed significant hemisphere-specific meta-control (indicated by asterisks).

right hemisphere-specific color pairs. In other words, there was no hemispheric asymmetry effect in response selection at the population level (t (15) = −0.227, p = .824). This was partly different at the individual level. For individual evaluations we only analyzed the individuals who responded to the ambiguous stimuli with more than 10 pecks. This left us with 11 individuals of which only 4 showed a significant individual asymmetry in terms of meta-control. These 4 birds responded significantly more often to one hemisphere-specific positive stimulus than the other. Based on chi-square analyses, three of these four birds had a right eye/left hemisphere dominance for meta-control (p < .01), and the other one had left eye/right hemisphere dominance (p < .05) (Fig. 2).

Reaction times of all trials were calculated after first excluding extreme values: We regarded extremely fast (faster than 200 ms) and extremely slow responses (beyond the standard deviation of the median) as outliers. Within the remaining data set, there were significant reaction time differences between the three stimulus types (gray/white: 80% of all trials; ambiguous: 10%, super-stimulus: 10%) of the first critical session (F = 13.77, p < .001) (Fig. 3). According to a Bonferroni correction, the source of the differences was the different reaction times between 'ambiguous' vs 'super-stimulus' (p = .004) and 'ambiguous' vs 'white/grey' stimuli (p = .001). These differences disappeared in subsequent sessions. Thus, pigeons had indeed delayed their responses to ambiguous stimuli in the first session of our test procedure. This makes it likely
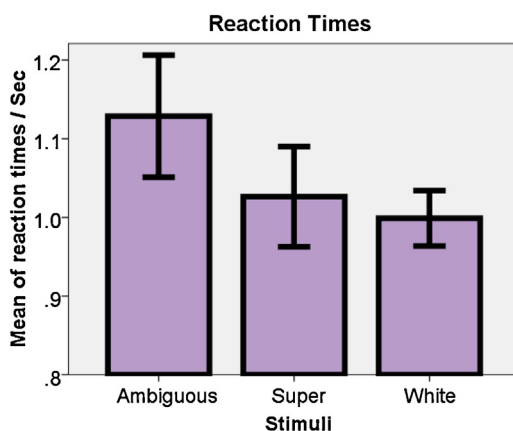
Reaction Times

Fig. 3. Average reaction time of subjects to the ambiguous, super, and white stimulus. Errors bar ±2 SE.

that our ambiguous stimuli induce a hemispheric response conflict that required a longer processing time before responses execution could take place. There was no significance reaction time difference between the super-stimulus and the white/gray stimulus. This was to be expected since the associative backgrounds of both stimuli were similar way for both hemispheres.

As outlined in the introduction, we assumed that a response conflict should also be visible in peck locations: When one hemisphere opts for the upper and the other hemisphere for the lower compound, the final peck position could deviate toward a middle spatial location, reflecting this conflict. For this study, we analyzed the peck positions of the animals during the critical first session according to Dittrich et al. (2010) [13]. The position of colors on the ambiguous keys could be arranged in four different ways that were used in a counter-balanced way and are depicted in Fig. 4a. As visible, the distance between the centers of the two S+ colors could either be very close (4.5 cm), medium (7 cm), or long (9.5 cm). If meta-control is associated with a response conflict, we should expect to see pecks on the S− colors between the two S+ colors, resulting from a simultaneous activation of two divergent motor plans. The farther away the two S+ colors from each other, the more pecks on the intermingled S− colors are to be expected. Indeed, the analysis of peck locations showed that the probability to peck on an S− color was proportional to the distance between the two S+ colors (Fig. 4b). When the distance between two positive colors were 9.5 cm, subjects produced significantly more responses to the S− colors than when the two S+ colors had a distance of 4.5 cm (X^2 test, p = .014). In contrast, during presentation of the super stimulus we practically never observed pecks on the S− (Fig. 4b). In addition, we observed that pigeons chose the upper compound as a default option when the two S+ colors were maximally distant (Fig. 4c).

To summarize our main findings, we could replicate the Go/NoGo-task based results for meta-control in pigeons of Adam and Güntürkün (2009) [5] with a forced choice paradigm. Meta-control data did not show a population bias toward one hemisphere, although a non-significant bias toward the left hemispheric dominance was visible. Most importantly, we found signatures of response conflict in reaction times and in the spatial response patterns of the animals. We will discuss these aspects, one by one.

The fact that meta-control is visible in humans [1–3], monkeys [4], and pigeons [[5], this study] makes it likely that the ability of a single hemisphere to control the entire response pattern is a basic function of vertebrates. The forced-choice based demonstration of meta-control in the current experiment deviated from the Go/NoGo design of Adam and Güntürkün (2009), but the basic results were essentially identical. Thus, the occurrence of meta-control is rather independent of the stimuli being shown successively or simultaneously.

Adam and Güntürkün (2009) [5] had observed that the left hemisphere gained meta-control dominance with increasing exposure time to the stimuli. With our forced choice procedure we had no possibility to observe meta-control responses for an extended period, but we also observed that more individuals tended to have a left hemispheric meta-control. This is possibly due to birds having a left hemispheric superiority to categorize visual stimuli [14]. This left-right difference at the behavioral level is possibly due to physiological [15], connectional [16], and morphological [17] differences within the pigeons' tectofugal pathway. This is similar to humans were either timing of hemispheric stimulation [2] or the lateralized category of chimeric stimuli [1] determines hemisphere-specific meta-control.

A main goal of the current study was to test the idea of inter-hemispheric competition as a means of meta-control. Indeed, the two eyes of birds project virtually exclusively contralaterally, such that in our task each hemisphere had learned different color discriminations. We had expected to see signatures of hemispheric
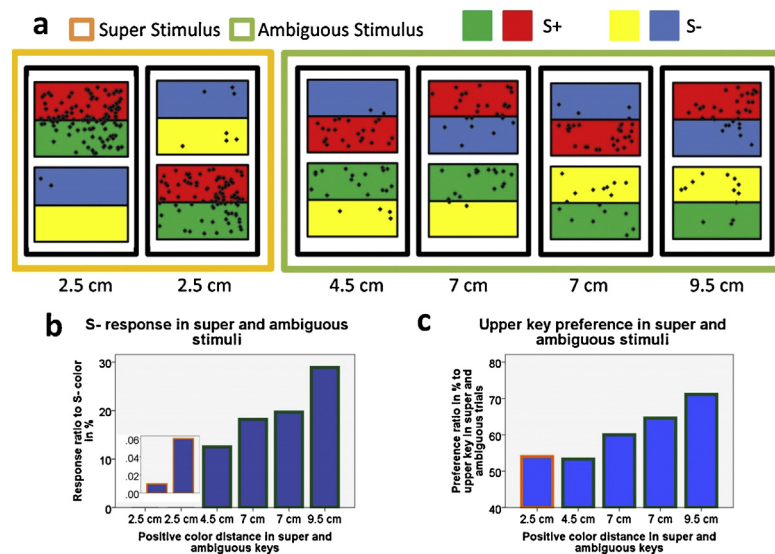
Fig. 4. Depiction of the peck locations in the two different arrangements of the super stimuli and the four different arrangements of the ambiguous stimuli. The colors displayed here (left eye: red S+, yellow S−; right eye: green S+, blue S−) represent only the combination used for a subgroup of animals. In fact, colors and their associative history were balanced among animals and hemispheres. (b) Displays S− responses as an indicator of spatial conflict based on the different arrangements of the super and ambiguous stimuli. The insert shows the very small amount of pecks onto S− during super stimulus trials in a magnified manner. (c) Displays the upper key preference that increased proportional to the distance between the two S+ colors. Each bar in (b) and (c) represents the color arrangements shown in (a) in the respective sequence. Additionally, in (c), the first bar represents both peck position for the super stimuli. (For interpretation of the references to color in figure legend, the reader is referred to the web version of the article.)

conflict in the reaction time data. Indeed, our pigeons needed longer to execute a peck under ambiguous stimulus conditions. It is usually assumed that response conflicts result in increases of reaction times, due to inhibitory interactions at very early [18] or later stages of processing [19]. Indeed, inhibitory hemispheric interaction models are often used to explain functional hemispheric asymmetries since differently specialized hemispheres could often generate discrepant response tendencies [8]. However, there is a class of models that make completely different predictions for experiments like the current one. These race models do not necessarily invoke inhibitory processes, but assume two independent response options in which each stimulus is separately processed [20]. When in our task color stimuli are displayed, these models would predict both colors to be processed in parallel and the peck being triggered as soon as the first color is detected. As a result, reaction time would result from the latency of a single detection process in monocular trials, whereas it would be determined by the winner of the two detection processes in binocular trials. Since the average detection time of the winning hemisphere in a race is expected to be shorter than the average detection time of a single hemisphere, a simple race model would predict a reaction time advantage for binocular trials [21]. Our data make these simple race models unlikely and therefore assume an inhibitory interhemispheric process at one stage of response execution. In humans, it is often assumed that this interhemispheric inhibition is realized via the corpus callosum [8]. Birds, however, have no corpus callosum but only a commissura anterior that interconnects the arcopallia of the two hemispheres [22]. The avian arcopallium has strong descending projections to subtelencephalic motor and visuomotor structures that control pecking movements [23,24]. We therefore assume that the delay in responding during ambiguous stimulus presentations probably generated an inhibitory interhemispheric interaction that overall slowed down the executed peck but gave one hemisphere meta-control over the other.

We assume that meta-control is not absolute and thus expected to also see the effect of interhemispheric conflict in the spatial positions of the peck patterns of the birds. Indeed, we could reveal that contradictory stimuli generated response patterns that possibly

represent an average of two near-simultaneously activated divergent movement trajectories. Indeed, similar conflicting movement patterns are reported in human literature when conflicting motor programs are initiated at about the same time [25].

Taken together both reaction time differences and spatial pecking patterns indicate that meta-control results from an interhemispheric conflict that is possibly generated by hemisphere-specific and contradictory response plans. The fact that we could show this in pigeons reveals that the commissura anterior is sufficient to enable fast interhemispheric interaction during response generation. This accords with previous results that hemispheric cooperation during choice reactions does not depend on the presence of a corpus callosum [26].

Acknowledgement

References

[1] Levy J, Trevarthen C. Metacontrol of hemispheric function in human split-brain patients. J Exp Psychol Human 1976;2:299–312.
[2] Lazarus-Mainka G, Hormann H. Strategic selection (metacontrol) of hemisphere dominance in normal human subjects, or: some neglected factors in laterality research. Psychol Res 1978;40:15–25.
[3] Urgesi C, Bricolo E, Aglioti SM. Hemispheric metacontrol and cerebral dominance in healthy individuals investigated by means of chimeric faces. Cogn Brain Res 2005;24:513–25.
[4] Kavcic V, Fei R, Hu S, Doty RW. Hemispheric interaction, metacontrol, and mnemonic processing in split-brain macaques. Behav Brain Res 2000;111:71–82.
[5] Adam R, Güntürkün O. When one hemisphere takes control: metacontrol in pigeons (*Columba livia*). PLoS ONE 2009;4:e5307.
[6] Vallortigara G. Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. Brain Lang 2000;73:189–219.
[7] Hoptman MJ, Davidson RJ. How and why do the two cerebral hemispheres interact. Psychol Bull 1994;116:195–219.
[8] Chiarello C, Maxfield L. Varieties of interhemispheric inhibition, or how to keep a good hemisphere down. Brain Cogn 1996;30:81–108.
[9] Zysset S, Muller K, Lohmann G, von Cramon Y. Color-word matching stroop task: separating interference and response conflict. Neuroimage 2001;13:29–36.

[10] van Veen V, Carter C. Separating semantic conflict and response conflict in the Stroop task: a functional MRI study. Neuroimage 2005;27:497–504.
[11] Gazzaniga MS. Cerebral specialization and interhemispheric communication. Brain 2000;123:1293–326.
[12] Rose J, Otto T, Dittrich L. J Neurosci Methods 2008;175:104–7.
[13] Dittrich L, Rose J, Buschmann JUF, Bourdonnais M, Güntürkün O. Peck tracking reveals focus of attention in pigeons. Anim Cogn 2010;13:133–43.
[14] Yamazaki Y, Aust U, Huber L, Hausmann M, Güntürkün O. Lateralized cognition: asymmetrical and complementary strategies of pigeons during discrimination of "human concept". Cognition 2007;104:315–44.
[15] Verhaal J, Kirsch JA, Vlachos I, Manns M, Güntürkün O. Lateralized reward-related visual discrimination in the avian endopallium. Eur J Neurosci 2012;35(8):1337–43.
[16] Güntürkün O, Hellmann B, Melsbach G, Prior H. Asymmetries of representation in the visual system of pigeons. NeuroReport 1998;9:4127–30.
[17] Güntürkün O. Morphological asymmetries of the tectum opticum in the pigeon. Exp Brain Res 1997;116(3):561–6.
[18] Brascamp J, Sohn H, Lee SH, Blake R. A monocular contribution to stimulus rivalry. Proc Natl Acad Sci U S A 2013;110(21):8337–44.
[19] Shen YC, Franz EA. Hemispheric competition in left-handers on bimanual reaction time tasks. J Mot Behav 2005;37(1):3–9.
[20] Marley AAJ, Colonius H. The 'horse race' random utility model for choice probabilities and reaction times, and its competing risks interpretation. J Math Psychol 1992;36:1–20.
[21] Schröter H, Fiedler A, Miller J, Ulrich R. Fusion prevents the redundant signals effect: evidence from stereoscopically presented stimuli. J Exp Psychol Hum Percept Perform 2011;37:1361–8, http://dx.doi.org/10.1037/a002428.
[22] Zeier HJ, Karten HJ. Connections of the anterior commissure in the pigeon (Columba livia). J Comp Neurol 1973;150(2):201–16.
[23] Wild JM, Arends JJA, Zeigler HP. A trigeminal sensorimotor circuit for pecking, grasping and feeding in the pigeon (Columba livia). Brain Res 1984;300:146–51.
[24] Manns M, Freund N, Patzke N, Güntürkün O. Organization of telencephalotectal projections in pigeons: impact for lateralized top-down control. Neuroscience 2007;144:645–53.
[25] Oliveira FTP, Diedrichsen J, Verstynen T, Duque J, Ivry RB. Transcranial magnetic stimulation of posterior parietal cortex affects decisions of hand choice. Proc Natl Acad Sci U S A 2010, http://dx.doi.org/10.1073/pnas.1006223107.
[26] Prior H, Wilzeck C. Selective feeding in birds depends on combined processing in the left and right brain hemisphere. Neuropsychologia 2008;46(1):233–40.