

cardiac explants demonstrated that cardiac myocytes can undergo DNA synthesis and mitosis in vitro while maintaining their contractility in long-term culture conditions.

Cell biologists have studied DNA synthesis and cell division of larval and embryonic cardiac myocytes in monolayer and organ cultures (10, 11). In our study, adult newt ventricles were cut into several pieces (0.5 to 1.0 mm) and cultured for 4 weeks at 25°C in a modified Leibovitz medium (L-15) supplemented with 10 percent fetal calf serum and 1 percent penicillin streptomycin. Since this growth medium contained a high concentration of basic amino acids as free bases (12), the amino acids substituted for the usual bicarbonate-CO₂ buffer system so that a constant pH was maintained in free gas exchange with the atmosphere. The explants (Fig. 1) were examined daily under a phase-contrast microscope for evidence of contractility of the cardiac myocytes. The ventricular explants were labeled for 24 hours with [³H]thymidine (1 μCi/ml) at 7, 14, 21, and 30 days after culture initiation; the labeling time was found to be suitable for sufficient access of tritiated thymidine to the cells for autoradiography. The explants were then cut into thin sections and processed for electron microscopic autoradiography.

The first interesting observation was the survival of the adult heart pieces in culture as evidenced by the beating of the pieces throughout the culture period. In the first week of culture, one third of the pieces established pulsation rates from 3 to 67 beats per minute. These rates did not change until the end of the culture period. The cut surfaces had become smooth and covered with flat cells and a layer of loose connective tissue, indicative of healing (Fig. 1, a and c). Examination of the autoradiograms revealed that dedifferentiated cardiac myocytes can undergo DNA synthesis and mitosis. The radioactivity in the nuclei of the cardiac myocytes was initially detected in a 7-day culture (Fig. 1b). The number of labeled nuclei in the cardiac myocytes gradually increased until a maximum was observed in the third week of culture, beyond which there was a decline in incorporation of [³H]thymidine. This implies that DNA synthesis in the cardiac myocytes began in the first week and gradually increased until a peak was reached in the third week, after which synthesis declined. Some of these cardiac myocytes exhibited mitosis, as is evidenced by the presence of mitotic chromosomes (Fig. 1c). Mitotic cells were observed throughout the

culture period. The trend of mitosis was similar to that of DNA synthesis. The maximum number of mitotic chromosomes was observed in the third week of culture, which was followed by a decline in the fourth week.

The cardiac nonmuscle cells, mostly fibroblasts and endothelial cells, also incorporated [³H]thymidine in their nuclei. The number of labeled nonmuscle cell nuclei was highest in the first week of culture but decreased gradually thereafter. The nonmuscle cells underwent mitosis and, as for the myocytes, the profile of mitosis was similar to that of DNA synthesis.

Since the mitotic activity is restricted to the dedifferentiated cells, which possess features characteristic of the embryonic cardiac muscle cells, the basic research question concerns the reprogramming of the adult cardiac myocytes with embryonic features of DNA synthesis and cell division. The reprogramming due to dedifferentiation is very important in the regeneration of the adult myocardium, since adult cardiac myocytes do not undergo DNA synthesis and mitosis under normal situations. The present findings provide evidence that the adult amphibian cardiac myocytes can undergo DNA synthesis and mitosis when explanted and cultured.

This study and our previous studies (8, 9) have cast light on the autorhythmicity of adult cardiac myocytes. Although the cells of our cardiac explants underwent dedifferentiation, the explants did not change the beating rate that they established when first placed in culture. What is the relationship between the morphological alterations in myofibrils and the

pattern of heartbeat in cardiac explants? Evidently the alterations that occurred were not great enough to affect heartbeat. Since embryonic cardiac muscle cells with patches of myofibrils and free myofilaments are capable of maintaining a sustained pulsation rate, dedifferentiated cardiac muscle cells, reminiscent of the embryonic cells, possessed the same kind of potential for maintaining sustained contractile properties. There is probably a need for a minimum amount of contractile proteins to maintain the contractile property of the cardiac muscle cells.

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13. This work was supported by a Michigan Heart Association grant-in-aid and by a National Institutes of Health basic research grant to Oakland University.

19 March 1979; revised 31 May 1979

Sociobiology of Bank Swallows: Reproductive Strategy of the Male

Abstract. *Male bank swallows pursue a mixed reproductive strategy. As previously documented, they form monogamous pair bonds with females with whom they will share parental duties of nest-building, incubation, and feeding of the young. In addition, however, they routinely seek promiscuous copulations with other females, both before and after pair-bonding.*

Trivers suggests that a monogamous male should be under selective pressure to pursue a "mixed" reproductive strategy when conditions permit: "to help a single female raise young while not passing up opportunities to mate with other females whom he will not aid" (1, p. 145). As a corollary, in such species the male should sequester his mate, that is, protect her from insemination by other

promiscuous males. In the course of a long-term study of the bank swallow, *Riparia riparia* (2), we have discovered that males of this species appear to routinely and actively pursue a mixed reproductive strategy (MRS). Some of the behavior patterns we have observed have been noted before and interpreted differently (3, 4), but we believe that our observations in sum can be more par-

simoniously interpreted as reflecting the operation and consequences of a male MRS. To the best of our knowledge this is the first documentation of an MRS as a persistent aspect of the social behavior of a nonhuman vertebrate species (5).

Bank swallows are insectivorous birds that hunt their prey on the wing, foraging over long distances from the nest (6). They live in large colonies, possibly because of the benefits of social foraging or predator defense, although this explanation is disputed (2, 6, 7). These colonies typically contain hundreds and sometimes thousands of individuals, who dig tightly packed burrows into sheer sandbanks; these banks occur naturally in cuts along waterways and, more commonly now, in man-made sand quarries. A pair builds its nest at the back of the burrow and raises a single brood there. The sexes are monomorphic, and the behavior of male and female has generally been described as identical in most respects as well (3, 4). For example, both sexes participate in nest-building, incubation, and feeding of the nestlings. At first glance, bank swallows seem the classic example of a monogamous, monomorphic bird species.

Two crucial conditions for a male MRS are present in bank swallows. (i) They live in large social groups, and (ii) within the colony as a whole there is little synchronization with respect to nesting-cycle state [though smaller groups within a large colony do show marked intragroup synchronization (6)]. Thus it is possible, theoretically at least, for a mated male to seek promiscuous copulations with females who have just paired and are about to lay eggs.

Our general method has been to color-mark and band 20 to 30 individuals in a colony and then systematically note the particular kinds of interactions they are involved in. Although there are a number of published studies of the social behavior of bank swallows, useful data on the relations of the sexes are scarce since the investigators have not systematically observed color-marked individuals whose sex was known (8). Our generalizations are based on observation of 252 color-marked individuals of known sex at 12 sites in Michigan and Massachusetts. These observations represent approximately 2000 observation-hours over eight breeding seasons (1970 through 1977). Our data base gives us reasonable confidence that our generalizations are not trivially population-specific.

The key observation is that for a 7- to 8-day period after pair formation (9), the male bank swallow pursues his mate on

each and every flight from the burrow (as many as 100 flights in one day) (Fig. 1). We interpret these chases as mate-guarding. On these flights, which may be relatively short flights to collect nesting material or foraging flights of $\frac{1}{2}$ hour or longer, the male stays very close to the female (generally within 1 m). Keeping close to his mate requires considerable agility on the male's part, owing to the

acrobatic nature of her flight. These spectacular pursuit flights are the most conspicuous feature of a bank swallow colony in its early stages. They were first clearly described by Petersen (3), who thought they were engaged in by mated pairs with the male as the chaser. We have confirmed this in observing more than 100 color-marked pairs: We have never seen an exception to the rule that

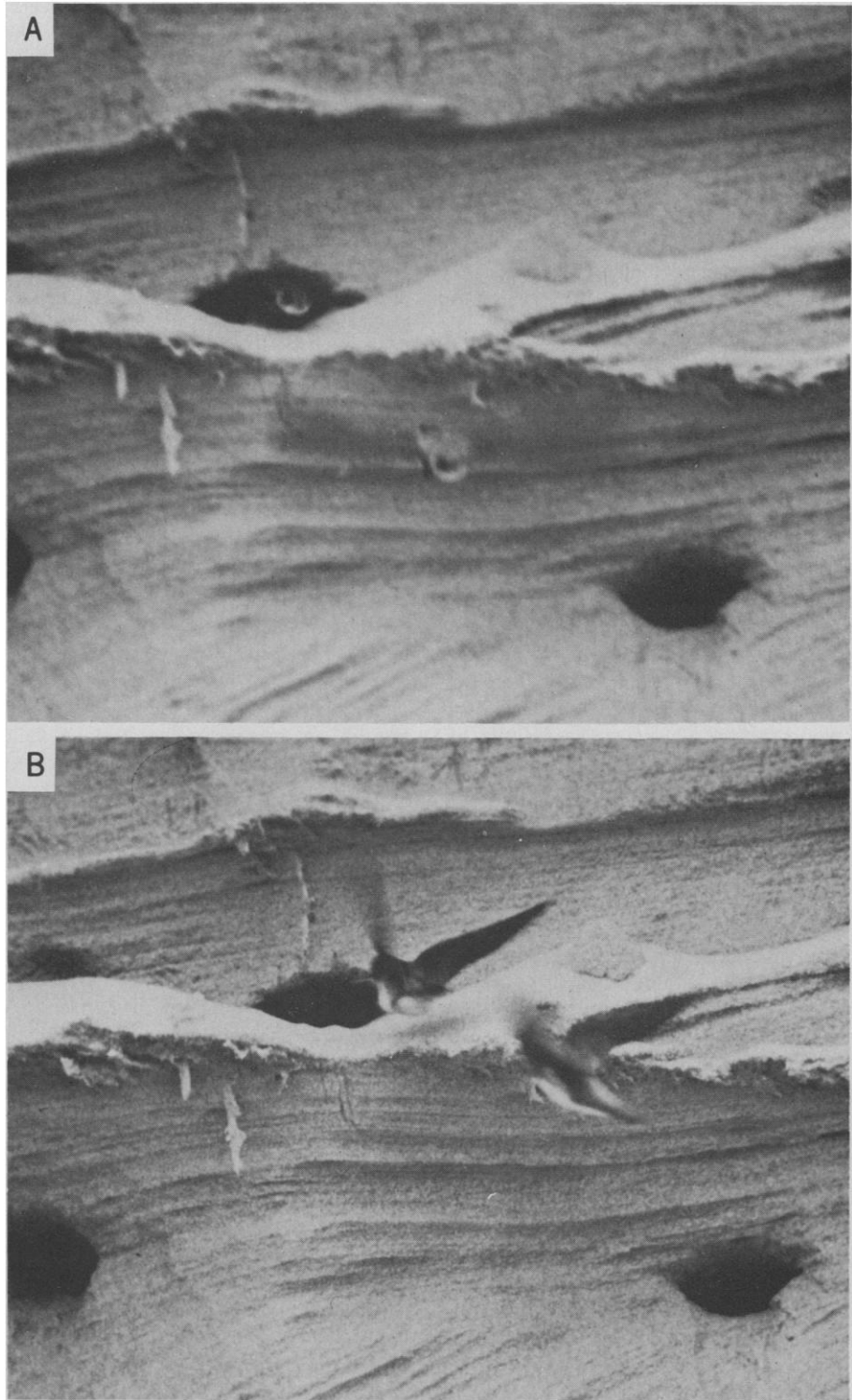


Fig. 1. Male chasing his mate from the burrow (A) and back (B). Note that the female is carrying a piece of nesting material on the return flight.

the male chases the female. Petersen gave these pursuit flights the apt name "sexual chases," but he interpreted them as courtship displays functioning to solidify the pair bond. This is a nice example of the differing interpretations afforded by the approaches of classical natural history and contemporary socio-biology (10), though these interpretations are not mutually exclusive.

Petersen also noted that on most sexual chases the pair is joined by one or more additional birds, but he was unable to determine the sex or other characteristics of these birds. We have been able to identify the sex of these additional chasers in more than 100 cases: they are always males. Thus a sexual chase typically consists of a female, her mate, and, over at least part of its course, one to five other males; all the males follow the intricate maneuvers of the female, giving the chase its spectacular appearance. We propose that sexual chases represent the two aspects of a male MRS: (i) the male's attempting to protect his mate from insemination by other males and (ii) other males' probing for opportunities for promiscuous copulations. We offer several lines of evidence to support this view.

1) Mated males as well as unmated males enter chases as additional chasers. Since males never have more than one mate, this indicates that the activity is not part of mate acquisition. One example is shown in Fig. 2, which gives typical data for one subcolony of ten color-marked pairs. All the males of this group entered chases as chasers (we distinguish for convenience between "chasers" and "guarders") both before and after the period in which they were otherwise occupied in guarding. The only exceptions we have observed to the rule that males resume chasing during incubation occur when the opportunity does not exist, namely for late-nesting (probably reneating) birds. That mated males consistently participate in these chases establishes this behavior pattern as part of an MRS, provided that there is some likelihood that such chases can lead to successful copulations.

2) Additional field observations (2) have established that male-male competition is involved in these sexual chases. On many sexual chases in which the pair is joined by one or more chasers, the male will loop back and attempt to fight off the chasers. Sometimes he merely bumps the chaser, but he may enter into a vigorous face-to-face fight. A most interesting case occurs when the pair flies out of the burrow directly into very heavy traffic (three or four chasers).

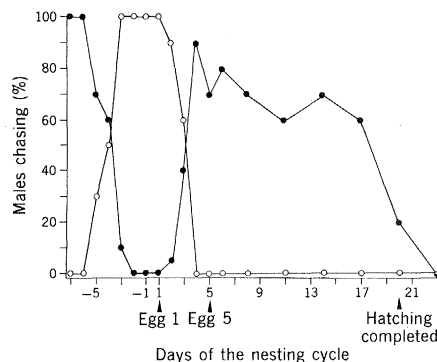


Fig. 2. Each data point represents the percentage of marked males in the subcolony ($N = 10$) that at least once on that day were observed to (i) chase their mate from the burrow and back (○), as in Fig. 1, or (ii) chase birds who were not their mates, typically females of other pairs (●). In the latter case, the male entered into the chase away from his home burrow, most often near a burrow of another pair. The numbers can add to more than 100 percent, since a male can do both on a given day (in fact, however, they typically are seen to do only one or the other on a given day). Note also that the "nonmate" category can include the female who later becomes his mate. Each day's data are based on four to six observation hours. The true percentage, of course, may be underestimated; this measure reflects the same effects, however, as other similar measures (for example, number of times a bird is seen chasing per hour) but is less influenced by sampling errors.

The guarding male may then overtake his mate and attempt to direct her back to the burrow. This he does either subtly by bumping her once or twice (to which she may or may not respond) or, more emphatically, by knocking her to the ground, or starting a face-to-face fight with her, and then heading her back to the burrow. We have witnessed these scenes many times; they were mystifying until we established the sexes of those involved. Occasionally the pair becomes separated; the male can then be seen searching for his mate, flying about the bank, and returning often to check out the burrow.

3) The male appears to restrict his guarding to the period in which his mate is fertile. This period cannot at present be identified precisely for passerine birds, but it probably begins 3 to 4 days before the laying of the first egg and ends about the day of the third egg (11). Mate-pursuit flights begin 3 to 5 days before the first egg is laid and end by the day the fourth egg is laid (Fig. 2) (12). Except for the few cases in which the pair becomes separated, a female makes no unescorted flights from the day of pairing until the day of the third egg (which corresponds approximately to the day she begins incubating), and then she makes very few of these until the clutch is complete.

4) Males restrict their chasing to females that are likely to be, or appear to be, in the fertile period. This is obvious with respect to their tendency to chase mated pairs, but it can also be seen in their chases of single birds: They chase only females, and they selectively chase females that are in the egg-laying stage or close to it. For the ten females of the colony described in Fig. 2, we calculated the percentage of flights on which they were chased. On days 3 to 8 they were pursued on 64 percent of their unescorted flights; on days 9 to 14, 8 percent; and on days 15 to 20, 1 percent. We believe that males can detect the heavier flight of reproductively advanced females, who may be as much as 20 percent heavier than normal in this period. Though chasing a heavy but single female would seem a bad bet, since it is highly likely that she is not in fact carrying fertilizable eggs (otherwise her mate would be guarding her), it may be worthwhile since females do occasionally become separated from their mates during the pursuit phase.

5) Males do attempt promiscuous copulations with females (13). Though we have seen chases end in copulation attempts by chasing males only three times, we think this reflects primarily (i) the difficulty of making these observations and (ii) the success of the guarding male. Chases continue as the birds leave the bank area and out of the observer's view. Thus the observer presumably sees only a small fraction of the total chase. We have developed the argument elsewhere (2) that a high incidence of promiscuous copulations is inconsistent with strong monogamous pair bonds in which the male invests heavily in parental care; that is, the two could not evolve together. The cost of a promiscuous copulation to the guarding male greatly exceeds the cost to the promiscuous male of seeking such opportunities (2, 14). The situation should be contrasted with that in mallard ducks, for example, where the pair bond dissolves after eggs have been laid (5). The cost to the guarding male is smaller for mallards than for swallows since the mallard male makes no further investment in the offspring after egg laying.

Considerable evidence suggests that the chasing male is seeking copulations, apart from the three cases we have seen and the circumstantial evidence given above. Many observers have reported promiscuous copulations by bank swallows with dead or stuffed birds (2, 3, 4, 7). Hoogland and Sherman reported that these copulations are particularly easy to elicit when a colony is in the nesting

stage, that only males participate, and that the semen can be found on the dead bird (7). In similar experiments (2), we have found that *mated* males participate in these promiscuous copulations. We have observed that any heavy flying bird elicits this "rape" reaction. For example, on a few occasions when a just-released, newly color-marked bird had difficulty gaining altitude, it was pounced on by a group of birds who then attempted copulations. Similar reactions occur when the bird is flying with difficulty for natural reasons (for example, when it is sick). We think this may be related to the heavier flight of egg-carrying females. A final point is that although the female's reproductive system regresses throughout incubation, the male's does not: his testes contain sperm until well into the stage in which he is feeding nestlings (3).

Previously many aspects of the social behavior of animals have gone unnoticed, been misunderstood, or been ignored because of the failure to recognize their potential function of maximizing the individual's inclusive fitness (15). We suggest that much of the social behavior of bank swallows is understandable only when viewed in the context of an MRS. This aspect of social behavior among bank swallows is so prominent that we suspect that closer investigation of the natural history of other monogamous species living under the appropriate conditions may reveal that an MRS is indeed a relatively common pattern.

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3. A. J. Petersen, *Wilson Bull.* **67**, 235 (1955).
4. A. C. Bent, *U.S. Natl. Mus. Bull.* **179** (1942).
5. Rape attempts have been reported in a number of duck species that are conventionally described as monogamous [D. P. Barash, *Science* **197**, 788 (1977); F. McKinney, in *Function and Evolution in Behavior*, G. Baerends, C. Beer, A. Manning, Eds. (Clarendon, Oxford, 1975), p. 331]. The male's reproductive strategy cannot be described as "mixed", however, at least in some of these species, since these males do not make any parental investment. The pair bond seems primarily to have the function, for the male, of enabling him to sequester the female. He does not help her build the nest, incubate the eggs, or feed or guard the young. Indeed, in duck species in which the male does provide some parental care, rape attempts are apparently rare [F. McKinney, in *Breeding Biology of Birds*, D. S. Farner, Ed. (National Academy of Sciences, Washington, D.C., 1973), pp. 6-21]. It seems probable, however, that in some of these duck species, field studies will reveal stable MRS's; for example, McKinney's study (1975) of green-winged teals in large pens is suggestive.
6. S. T. Emlen and N. J. Demong, *Science* **188**, 1029 (1975).
7. J. L. Hoogland and P. W. Sherman, *Ecol. Monogr.* **46**, 33 (1976).

8. One reason for the lack of data is the difficulty of sexing bank swallows. The only reliable basis for sexing is the brood patch, which only the female has. We capture the birds and color-mark them before pairing and then recapture them during incubation to determine (retroactively) the sex of the members of the pair.
9. We say pair formation has occurred when the pair is seen to move in and out together. Before this time both individuals may be seen at the nest, but they fly in and out independently of one another. Typically other females are present as well, and the male has no apparent favorite. We believe that copulation, occurring within the burrow, may be the key event in triggering the change from one state to the other.
10. Hoogland and Sherman (7) noted pairs leaving and entering the burrow together in the first part of the nesting cycle, which they interpreted as mate-guarding, as we do. Though they believed males guarded females, they were not able to determine who was guarding whom since they had no color-marked, known-sex pairs.
11. P. D. Sturkie, *Avian Physiology* (Springer-Verlag, New York, 1976), p. 388. Most of the available data are from domestic ducks and chickens. In addition, there has been no research on sperm competition, so it is impossible to make strong generalizations.
12. The data in Fig. 2 are not confounded with time since (i) day 1 represents different days for the different pairs (range May 14 through May 22), and (ii) it was an early subcolony. Other sub-

colonies arose at several points during the nesting cycle of the subcolony described in Fig. 2, so there were always females to be chased and males to chase.

13. We have no idea if these copulation attempts are successful. It seems unlikely that in this species the question can be directly answered. F. McKinney (personal communication) has described research with ducks directed toward direct assessment of the outcomes of "rape" attempts.
14. In this paper we have considered only the reproductive strategy of the male. The female's perspective is different, of course. We will consider it in detail elsewhere (2). We note here only that a promiscuous copulation entails a considerable cost to the female's mate but, generally, not to her since her offspring's relation to her is independent of who the father is. There can be indirect costs to her; for example, her mate might detect and not provide parental care to the "illegitimate" offspring. So far as we know there are no such indirect costs to the female in bank swallows.
15. S. Blaffer Hrdy has discussed this phenomenon [*The Langurs of Abu* (Harvard, Cambridge, 1977)] in connection with observations of infanticide in langurs and other primates.
16. We thank J. Alcock, C. Brown, S. Cohen, and P. Schwagmeyer for critical comments on the manuscript.

20 September 1978

Cerebral Specialization, Writing Posture, and Motor Control of Writing in Left-Handers

Abstract. *It has been suggested that the inverted hand position of left-handers during writing indicates the left hemisphere of their brain is linguistically specialized and that the writing of these left-handers may be controlled via ipsilateral pathways. Electroencephalograph alpha asymmetry measures at central and parietal leads, as well as dichotic tests, differentiated right-handers from left-handers, but not inverters from noninverters. Electroencephalograph differences between hand posture groups did appear, but only at occipital leads during reading and writing tasks. Regardless of hand posture or speech lateralization, the right central region of the brain is significantly involved in the control of left-handed writing.*

Left-handers vary in their pattern of hemispheric specialization. Most studies agree that at least half of the left-handed population processes language primarily in the left hemisphere, as do most right-handers. There is less agreement about the amount of right hemisphere participation in language in the remainder of the left-handed population, and this group is typically described as composed of individuals whose specialization for language is either "bilateral" or "reversed" (1-5).

Levy and Reid (6) have reported that hand posture during writing in left-handers "can reliably predict which hemisphere is predominantly linguistic and which [is] primarily 'spatial.'" They described two distinct commonly used hand postures: the inverted position (IHP) in which the hand is held above the line and the pencil points toward the bottom of the page, and the noninverted (NHP) in which the hand is held below the line and the pencil points toward the top of the page. By using tachistoscopic measures, they demonstrated that right-handed subjects (except for one right-

hander who used IHP) and left-handed IHP subjects showed a superiority of the right visual field on a verbal test (nonsense syllable recognition) and of the left visual field on a spatial test (dot localization). The left-handed NHP group showed the opposite field advantages. Levy and Reid conclude that the linguistically specialized hemisphere is ipsilateral to the writing hand in the IHP group and contralateral in the NHP group. Further, Levy and co-workers speculate that the writing hand of the IHP group is controlled via ipsilateral pathways (6, 7).

It would be very useful to have a simple noninvasive technique to identify the linguistic hemisphere. However, researchers do not completely agree that hand posture can be used as such a general index. Moscovitch and Smith (8) used Levy's tachistoscopic measure and replicated the results (6, 7), but on a dichotic test they found no difference between hand posture groups. They also found that IHP writers react faster to visual hemifield targets with the ipsilateral hand, suggesting ipsilateral motor control. However, they failed to obtain the