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KINEMATIC SYNERGIES FOR THE CONTROL OF HAND SHAPE

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INTRODUCTION

The hand is one of the most studied biological systems, yet the strategies used by the Central Nervous System (CNS) to control object grasping and manipulation are not well understood. The main obstacle in understanding the control of the hand is its elaborate biomechanical (16, 26) and neural architecture (19, 20). This, in turn, presents obvious advantages and disadvantages. The most striking advantage of the hand's structural complexity lies in its ability to assume a uniquely rich repertoire of postures (18) that can mold and exert forces onto virtually any object shape. At the same time, however, this complexity might require a very large number of control strategies, thus imposing a significant computational load on the CNS.

Since the early classifications of hand posture proposed by Napier (18), researchers have adopted a variety of approaches to gain insight into the neural control of the hand. One such approach has focused on hand kinematics during the reach to grasp movement, particularly on the temporal evolution of two-digit grasp and the modulation of finger span as a function of object properties (5, 10-12, 17). Intuitively, the control of grasping using the entire hand would appear to be characterized by a higher degree of complexity, due to the larger number of degrees of freedom (i.e., muscles, joints) that has to be coordinated.

To characterize the control strategies underlying the control of hand shape as a function of object geometry, a number of recent studies has focused on the spatial and temporal coordination of finger motion during reaching and grasping (21-24). This paper deals with kinematic evidence indicating that the control of hand posture is characterized by consistent covariations, i.e., synergies, in the excursion of multiple joints of the digits (some of the results discussed in this paper have already appeared in published form (21-24)). These kinematic relationships thus effectively reduce the number of mechanical degrees of freedom that has to be controlled independently. As such, these synergies – emerging in both spatial and temporal domain – are likely to simplify the control of hand posture.

Experimental tasks and data analysis.

The results of three experiments on the control of hand posture will be summarized here: 1) hand shaping during reach to grasp objects with different shapes (24), 2) control of static hand configuration (21) and 3) the effect of sensory modality on the temporal evolution of hand shape (22). Experiment 1 focused on the extent to

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which hand shaping during reaching takes into account object contours. For Experiment 2, subjects were asked to reach and shape the hand as if to grasp and use a large variety of imagined objects. Experiment 3 also focused – as Experiment 1 – on the temporal evolution of hand shape, however this study was designed to characterize in more detail the kinematics of hand shaping during the reach.

An additional aim of Experiment 3 was to assess the influence of sensory cues on the control of these synergies. For this experiment, three tasks were studied: *a)* memory-guided reaches in which the object was not in view during the movement, *b)* virtual object, in which a virtual image of the object was projected in front of the subject and remained in view during the reach, but the object was not physically present, and *c)* real object, in which the object was in view and physically present. For Experiment 1, subjects were asked to grasp a number of objects with shapes ranging from convex to concave. For both experiments 2 and 3 objects spanning a wide variety of shapes and sizes were selected to best characterize the modulation of hand posture in the spatial and temporal domain.

Hand posture was measured by 15 sensors embedded in a glove (CyberGlove; Virtual Technologies, Palo Alto, CA). We measured the angles at the metacarpal-phalangeal (*mcp*) and proximal interphalangeal (*pip*) joints of the four fingers as well as the angles of abduction (*abd*) between adjacent fingers. For the thumb, the *mcp*, *abd* and interphalangeal (*ip*) angles were measured, as was the angle of thumb rotation (*rot*). Discriminant analysis (21, 22, 24) was used to assess the extent to which hand postures could be discriminated as a function of object geometry. We used linear regression analysis and principal components analysis to characterize the patterns of covariation between the angular excursions of the digits in the spatial (21) and temporal domain (22).

Modulation of hand shaping as a function of object contours during reach to grasp.

When grasping with two digits, the digits extend to a maximum aperture larger than the object about midway in the reach. A well documented feature of two-digit grasping is that the maximum finger span attained during the reach is linearly related to object size (5, 10, 11, 17). This finding indicates that the dimension of the object is taken into account before contact with the object is made.

When reaching to grasp objects with different shapes, the control of the entire hand posture during the reach might be controlled by two alternative strategies: 1) the shape of the object could be ignored, and the hand might simply mold to the object at the end of the reach; or 2) object shape might be used to scale hand posture during the reach, as found for grasping objects with different sizes. If this were the case, a close correspondence between hand configuration and object shape should emerge during the reaching movement.

From a qualitative point of view, the general pattern of pre-shaping of the entire hand resembles the gradual opening and closure observed for two digit grasping (21, 22, 24) (Fig. 1). However, discriminant analysis showed that neither of the two hypothesized strategies were used, as the hand molds only gradually to object shape

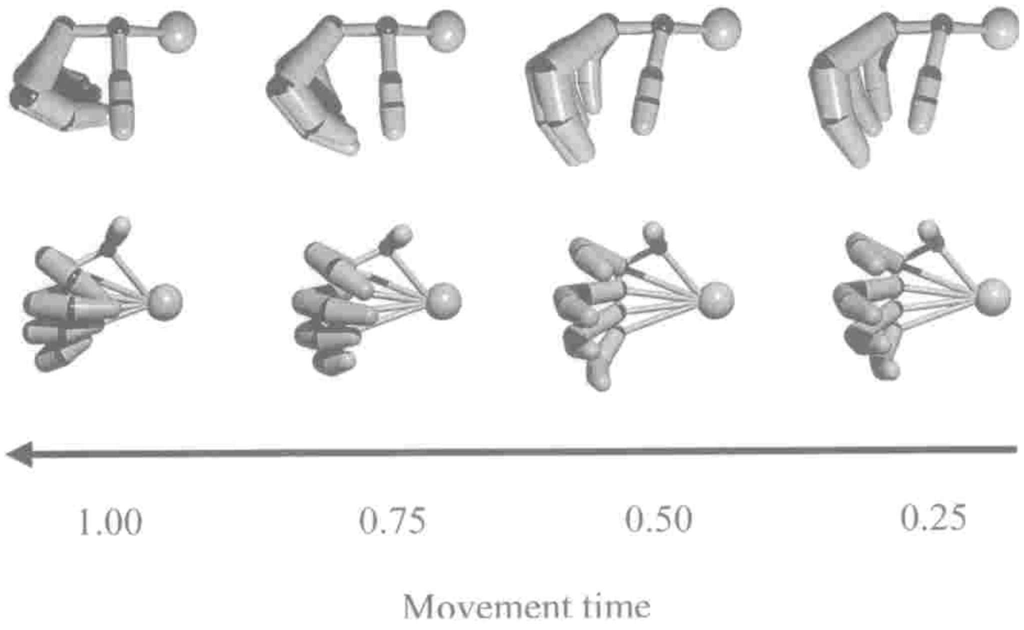

Fig. 1. - *Hand shaping during reach to grasp.*
The kinematic data were used to render a 3-D image of the hand during reach to grasp a beer mug (data are from one subject, Experiment 3[22]). A top and side view of the hand show how the hand gradually opens midway in the reach and then closes as it approaches the object. Also note how motion at all fingers occur in parallel.

as it approaches the object (24), maximum discrimination of hand posture being reached at contact with the object. In other words, fine modulation of hand posture occurs in a sequential fashion during the reach. Consequently, hand posture as a function of object shape is not specified fully at the time of maximum hand opening.

Temporal evolution of hand shape during reaching.

A more recent study on the temporal evolution of hand shape during reaching to grasp object with different shapes and sizes (22) has extended the above observation while revealing further aspects of the coordination patterns of finger motion. Strong covariations were found in the time courses of finger joint rotations, especially between *mcp* and *pip* joints (this feature can be noticed in Figure 1). The fact that not all the finger joints were controlled independently points to a reduction in the number of mechanical degrees of freedom. Principal components (PC) analysis, computed on the temporal waveform of the joint rotations, revealed that the first 2 principal components could account for a large proportion of the variance (74%) of the data. This finding further stressed that there was a high degree of similarity in the time course of finger motion when reaching to grasp objects with different sizes and shapes.

However, the most significant contribution of PC analysis to the interpretation of the data consisted of a revealing interaction between the first two components and their effect on hand configuration. Specifically, the major features of the first PC were that all digits gradually extended and flexed together, reaching a maximum excursion at the same time, i.e., at ~ 50-60% of the reach duration. This pattern occurred while the digits gradually abducted and later adducted toward the end of the reach. The pattern of motion of the PC2 was, however, dramatically different than that of PC1. Although motions at all *mcp* and all *pip* joints were still characterized by similar time courses, hand posture was relatively static until about 70% of the movement time, followed by a simultaneous extension of the digits. These data show that the two overlapping coordination patterns differentially affected hand configuration as the hand approached the object. Specifically, maximum hand opening was determined primarily by the first PC, whereas the finger span at movement's end was determined by the first and the second PC. Therefore – in agreement with the results of the above study (24) – there was not a unique correspondence between the hand posture attained at maximum finger span and the final static posture.

Sensory cues responsible for the gradual shaping of the hand.

One of the questions related to the temporal evolution of hand shape (24) was its dependence on sensory cues, the most likely candidate being vision. Vision of the hand and/or the object during the reach might have provided an 'error signal' leading to a gradual correspondence between hand posture and object contours. However, a similar discrimination of hand posture as a function of object geometry was found when reaching to grasp remembered objects and objects that were in view during the reach (22). A gradual discrimination of hand posture has also been reported when vision of the hand and the object is blocked at random times during the reach to grasp objects with different shapes (31).

Taken together, these findings suggest that vision is not used to modulate hand posture to object geometry. This is in agreement with the results of a recent study of eye and hand movements (13) indicating that subjects fixate the object during reaching, rather than the moving hand even as the hand approaches and contacts the object. Thus vision may be important in defining the location of an object and for monitoring changes in its location, size and orientation and less so for defining an error signal derived from the shape of the hand and of the object (2, 27).

With regard to the effect of physical presence of the object vs. reaching to grasp a virtual object, we found that a major effect was found only on the static hand posture at the end of the reach. This was indicated by the fact that higher order PCs were required to account for the variance around the time of hand closure. One possible interpretation of this finding is that once contact with objects of varying sizes and shapes was made, finger movements became more individuated, requiring a greater number of principal components to represent the hand posture.

Control of static hand posture.

When subjects were asked to match object size by molding hand shape, it was found that only two PC's could describe how hand postures were scaled to the dimensions of the object, despite large differences in object sizes and the number of digits used (23). This observation lead to the design of a subsequent study to characterize the control of static hand posture as a function of both object size and shape (21). It was found that static hand configurations at the end of a reach to grasp imagined objects were characterized by consistent patterns of joint-specific covariations of angular excursion. These covariation patterns exhibited similar features as those described for the time course of joint rotations among *mcp* and *pip* joints as described above. PC analysis revealed a high degree of similarity among the measured hand postures ($n = 57$), despite the wide range of object sizes and shapes used for this task. Specifically, the first two PC's – which were consistent across all subjects – could account for ~ 84% of the variance (Fig. 2). Therefore, all hand postures shared similar (few) relationships among the many mechanical degrees of freedom of the hand. PC1 captured the main patterns of covariation described above, whereas PC2 was characterized predominantly by a combination of *pip* joint flexion and *mcp* joint extension. (It should be noted, however, that discriminant analysis showed higher order PC's, i.e., higher than 2, to add significant information about hand posture, despite the small variance they accounted for).

The most surprising finding was that hand postures were distributed along a continuum when plotted in PC space defined by the first two PC's, rather than clustering in discrete groups as one might expect from the wide variety of object sizes and shapes grasped. Based on Napier's early classification of hand postures (18), one would have expected small objects – that are grasped with precision grips (i.e., chalk) – to elicit very different hand postures than those used to grasp larger objects (i.e., wrench), normally grasped using a power grip. However, PC analysis showed

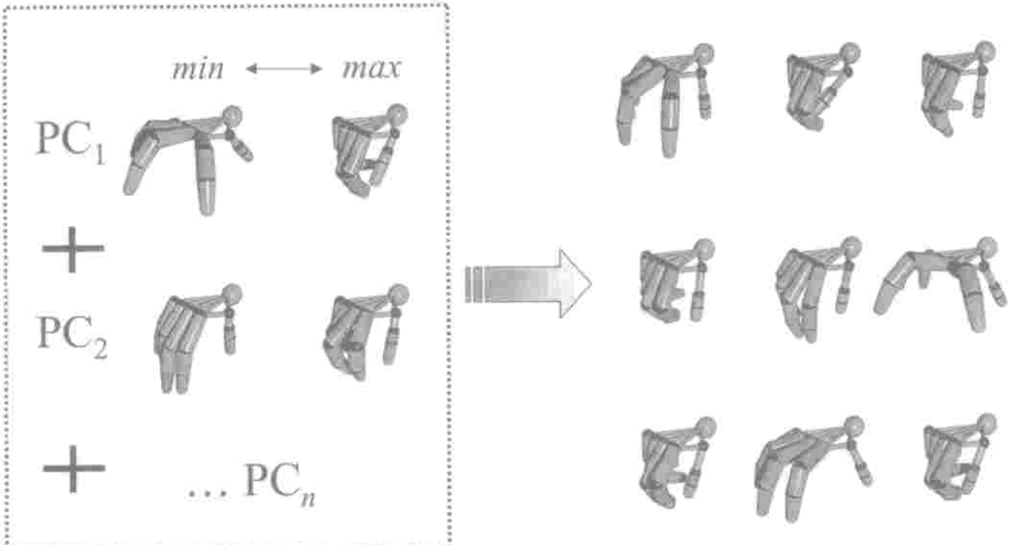

Fig. 2. - *Hand postural synergies.*
The left side of the figure shows the first two principal components computed on the static hand postures (shown on the right side) measured from one subject (Experiment 2[21]).

that a classification based on the kinematic relationships among finger joints revealed a high degree of similarity between hand postures used to grasp objects that varied widely in size and shape. Although our classification of hand posture would seem to be in conflict with previous hand posture taxonomies (6, 7, 14, 15, 18), it should be noted that these have used classification criteria that were different from ours. Specifically, Napier's well-known classification of power and precision grip was based on functional considerations, i.e., the amount of contact forces that a given hand posture is intended to exert on the object – a criterion that roughly correlates with the number of digits used. Our classification, however, was based on the quantitative measurements of hand postures. The different clustering of hand postures therefore implies that there is no one-to-one correspondence between hand posture and force control.

Functional implications of hand postural synergies.

Lower order PC's would seem to be responsible for a coarser level of hand posture control, where most degrees of freedom are controlled as a unit. In contrast, higher order PC's would represent overlapping synergies providing a higher individuation of finger motion, hence a finer modulation of hand configuration to object contours (Fig. 2). These findings generate compelling new questions. What are the neural correlates of these postural synergies? Can we think in terms of PC's when probing the CNS to understand the control of complex movements? Alternatively, is PC analysis's usefulness limited to detecting patterns in large bodies of data?

It is very tempting to speculate that PC's might represent the overt correlate of neural mechanisms underlying the coordination of multi-joint movements. Obviously, caution should be observed when inferring neural mechanisms from PC data (9) alone. Nevertheless, several studies of a variety of motor tasks have revealed the existence of a few, basic coordination patterns in the kinematic domain (1, 4, 28), as well as in the force (3, 25) and EMG domains (8, 29, 30). Although more research is needed to define the structure-function relationship of these synergistic mechanisms, the above evidence suggests that the exquisite versatility of the motor control system might rely on combining small number of synergies.

CONCLUSIONS

Despite the complex neural and biomechanical structure of the hand, kinematic synergies constraining the motion of individual digits have been characterized in a variety of grasping tasks involving the entire hand. A remarkable feature of these synergies is that a few coordination patterns (i.e., principal components, PC's) can describe a large number of different hand postures in the spatial and temporal domain, thus leading to a reduction in the computational load imposed on the CNS.

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