Representations automatically evoked by a depicted hand

by

Morgan Teskey
B.Sc., University of Calgary, 2015
M.Sc., University of Victoria, 2017

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We acknowledge and respect the ləkʷəŋən peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Supervisory Committee

Dr. Michael Masson, Co-Supervisor
Department of Psychology

Dr. Daniel Bub, Co-supervisor
Department of Psychology

Dr. Sandra Hundza, Outside Member
Department of Exercise Science, Physical & Health Education

Abstract

A conflicted and contentious literature has emerged from the proposal that visuospatial information from static images can automatically trigger associated motor representations. Curiously, investigations into this visual-motor relationship have predominantly focused on images of manipulable objects, while relatively little work has made use of images of body-parts- whose referents are represented directly in the motor system. Limited work has made use of hand images as task-irrelevant primes, in an effort to determine whether a hand image automatically evokes a motor representation of the viewer's corresponding limb. The results of these studies have provided diverging evidence and have resulted in competing theoretical accounts. Here, I present results from a series of stimulus-response compatibility experiments that were designed to probe the nature of representations generated by static hand images, while also addressing potential methodological weaknesses of the previous works. The results show that both stimulus properties and task demands influence the way in which an image of a hand is coded. Notably, I provide clear evidence that motor representations can be evoked automatically by depictions of particular hand postures, but that these representations are not an automatic, ineluctable component of the general processing of any hand image. These results not only contribute to a more unified account of hand representations, but also have wider implications for our understanding of the conditions under which static displays can engage motor representations.

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General Introduction

The way in which we internally represent and interact with our environment largely relies on a critical interplay between our visual and motor systems. For example, if someone were to toss an apple to you, catching it would require the execution of a motor plan – which would include a representation of action features such as the identity of the acting limb. Selection of particular features of the motor plan would inevitably be informed by visual input, which in this example would include visuospatial information about the apple's location relative to your body. This type of close interdependence of vision and action is emphasized in many theories, including the highly influential hypothesis that the visual system has a dedicated processing stream for information relating to mediating action (Goodale, 2011; Goodale & Milner, 1992). Moreover, there is evidence that action planning itself can modulate activity in V1 and other early visual areas, even under conditions in which the planned actions are not actually executed (Gutteling et al., 2015). Of particular relevance to the current discussion is the question of whether visuospatial information from static displays can be represented in a motoric fashion, even in the absence of an intention to interact with the depicted object.

The process of encoding visuospatial properties of a stimulus has been most extensively studied in the context of Stimulus-Response Compatibility (SRC) effects. One of the best-known and reliable SRC effects is the Simon effect (Simon, 1968). In a typical visual Simon task, a cue is presented on the left or right side of a computer monitor. Participants are tasked with generating a speeded left/right keypress response to classify some non-spatial property of the cue, such as its colour, according to an arbitrary response-key mapping. Though the spatial location of the cue is task-irrelevant, responses are made more quickly when the cue's location is congruent with the location of the response key, compared to when it is incongruent (Craft & Simon, 1970). This result has been obtained with a variety of other non-spatial cues, such as geometric shapes (Umiltà & Liotti, 1987) as well as with cues carrying spatial information, such as arrows or the words *left* and *right* (see Lu & Proctor, 1995, for a review). The conventional interpretation of such effects is that under these conditions both a spatial stimulus code and a spatial response code are formed and responses are slowed when the stimulus and response codes conflict, compared to when the features of these codes overlap (e.g., Kornblum et al., 1990; Zorzi & Umiltà, 1995).

Further investigations of SRC effects have aimed to clarify the mechanisms responsible for producing these effects. Consider that response codes are typically labeled in terms of left/right spatial dimensions, which lack any description of the nature of the representations underlying these codes. Does a left response code refer to, for instance, the relative location of the left response key compared to the right response key? Or could perhaps a left spatial code refer to the location of the responding hand on the response key relative to the observer's body, or even refer to the anatomical identity of the limb itself (left/right hand)? In a typical Simon-like paradigm all of these dimensions correspond with one another, which does not allow for specific conclusions to be drawn about the nature of the response codes. Wallace (1971) addressed this issue by having participants make responses with their hands crossed, such that the left hand depressed a right-sided key, and the right hand depressed a left-sided key. Under these conditions, the location of a response key was misaligned from the anatomical identity of the response hand. Responses were made more quickly when the location of the stimulus corresponded to the location of the response key, and not to the laterality of the response hand. Similarly, when participants made keypress responses by manipulating crossed or uncrossed sticks, held by hands in an uncrossed position, the Simon-effect went with the location of the response key, not the hand operating the stick (Riggio et al., 1986). Hommel (1993) further elucidated the nature of response codes in SRC paradigms by demonstrating that response codes reflect the goal of the response action, rather than its manner. In Hommel's task, pressing a key caused a light to flash on the side of space opposite to the response key. Participants were instructed either to "press the left/right key" or to "flash the right/left light" to respond to a cue. Participants who received the key-based instructions showed a typical Simon effect, but those who received the light-based instructions showed a reversed Simon-effect. That is, they were faster to respond when the spatial property of the cue corresponded to the location of the light, and not to the location of the response key, indicating that the response code was generated based on the goal, not the manner of the action. Of course, in a typical Simon task, the response action (pressing a key) corresponds to the response goal (the key being depressed). Taken together, these results show that spatial response codes generated in a typical Simon task correspond to the location of the response key in extrinsic space, rather than the anatomical properties of the effector producing the response action.

Another way to conceptualize the nature of the spatial codes that contribute to SRC effects is to describe the frame of reference in which the spatial properties of the stimulus are coded (Colby, 1998; Lu & Proctor, 1995; Umiltà & Liotti, 1987). Broadly speaking, there are two general reference frames that we use to represent spatial information. Extrinsic frames of reference make use of a coordinate system external to the observer.

With few exceptions (described in more detail below), visual SRC effects reflect the use of an extrinsic reference frame, as evidenced by the response time advantage generated by a leftward-positioned stimulus on a left-sided keypress, irrespective of which hand is used to press the key. In contrast, an intrinsic or body-based frame of reference makes use of a coordinate system referenced to the observer's own body, or parts of their body. Evidence for the use of an anatomical reference frame in SRC paradigms is reported primarily in the domain of tactile processing. For example, when participants made responses with foot pedals to classify the intensity (high or low) of a tactile stimulus delivered to either the left or right hand, they responded more quickly under conditions in which there was correspondence between the anatomical identity of the stimulated and the response limbs (e.g., the left hand and the left foot), regardless of the spatial relationship between the location of the stimulation and the location of the response in external space, which was manipulated between experiments by crossing and uncrossing the hands and feet (Medina et al., 2014). Not only is the use of such an anatomical reference frame seen less often in the visual domain, when visual and tactile trials were mixed within a single study, the visual SRC effect was obliterated, while the tactile SRC effect remained intact (Ruzzoli & Soto-Faraco, 2017). This finding is likely not due to the mixed-modality of the trials themselves, because when visual cues were mixed with auditory cues (which are also coded according to an extrinsic reference frame) SRC effects were found for both types of stimuli. Rather, the obliteration of the visual SRC effect might suggest that participants did not switch between reference frames from trial to trial based on the modality of the cue, but may have selected a single frame of reference based on overall task-demands.

Despite the general robustness of the claim that visual SRC effects reflect extrinsic spatial coding, there remains one domain in which researchers widely oppose this principle. Proponents of embodied cognition claim that depictions of objects automatically evoke effector-specific anatomical motor representations corresponding to the limb that one would use to interact with a depicted object, via affordances (e.g., Tucker & Ellis, 1998). For instance, an image of a frying pan with a handle protruding to the left is said to afford a left-handed action and, by extension, facilitate a keypress response made with the left hand. Although this idea is still widely accepted in the field, the evidence in support of the claim that SRC effects generated by an image of a graspable object are effector-specific remains unconvincing (e.g., Proctor & Miles, 2014). A number of methodological problems plague this issue, in addition to conflicting findings from studies that obtain either no SRC effects to handled objects under keypress conditions (Bub & Masson, 2010), reverse compatibility effects (Cho & Proctor, 2011), or clear evidence that object-based SRC effects reflect extrinsic spatial codes rather than anatomical effector-based codes from paradigms utilizing crossed-hand or foot responses (Phillips & Ward, 2002).

There are two notable task conditions under which effector-specific codes reliably appear to underlie SRC effects generated by images of handled objects. First, when participants made responses to images by executing a reach-and-grasp action on an external response element, SRC effects emerged, even though the same images did not produce effects under keypress conditions (Bub & Masson, 2010; Bub et al., 2018). These findings suggest that motoric representations are activated when observers are in an intentional state in which they prepare and perform goal-directed actions. The second task condition that has produced evidence for anatomical coding of images of handled objects involves the judgment of the laterality of a depicted hand. When participants made speeded keypress responses to classify the laterality of a hand image superimposed on a graspable object, the effect of compatibility between the object's handle and the response appeared to be effector-specific (Bub et al., 2021; Ullrich, unpublished thesis). Taken together, these results provide a key insight into the relationship between visual processing and motor representations, and suggest that static images might evoke motor representations when observers are utilizing motor representations to meet task demands. Such motor representations appear to be generated by motor intentions in the case of reach-and-grasp responses, and as part of the process of making an explicit hand laterality judgment. The interpretation that hand laterality judgments involve evoking motor representations is consistent with a wealth of evidence from studies on laterality judgments, such as that of Parsons (1994), discussed in more detail below. A most interesting question naturally follows from this work: are motor representations automatically evoked by the presence of a hand image, or are the task demands of making explicit laterality judgments responsible for generating visuomotor codes under these conditions?

Our understanding of the relationship between images and motor representations has been burdened by the uncertainty and complexity of previous work focusing on images of handled objects. It seems as though if one wanted to create optimal conditions to search for motor representations evoked by images, the most logical place to start would be not with handled objects, but with images of hands themselves. Our hands, like other body parts, but unlike handled objects, are represented directly and specifically in the motor system (Bracci et al., 2010). Additionally, we have extensive daily experience viewing our hands in action, during which time visual and sensory input from our hands is coordinated with our motor output. Further, our visual system devotes resources that appear to be exclusive to hand representations, as evidenced by the presence of hand-selective areas in lateral occipitotemporal cortex, which show view-invariant posture-sensitivity (Bracci et al., 2018). Additionally, hands have highly lateralized visual forms, which allows for hand stimuli to be assessed using relatively straightforward SRC methods, as does the fact that keypress responses can be made simply with an observer's own hands.

Seminal work investigating the nature of hand representations suggests that viewed hands can be mapped to an observer's body in a motoric fashion. Parsons (1994) provided evidence that the process of explicitly judging the laterality of a viewed hand is subject to restrictions akin to those restricting mimicry of the depicted posture, which arise due to the biomechanics of the human body, reflected by the pattern of response times to judge the laterality of various postures. This result suggests that producing a laterality judgment is reliant on the evocation of a motor representation of the depicted limb. Parsons developed a model of laterality judgments that remains widely accepted. This model proposes that the image of a hand automatically and pre-attentively evokes a motor representation of the observer's corresponding hand, and that a laterality judgment is made via a confirmatory matching process following the mental manipulation of this motor representation. Consistent with this model, de Lange et al., (2006) found that activity in the parieto-frontal network associated with laterality judgments increased according to the biomechanical complexity involved in the mental rotation of the image, even when the absolute degree of stimulus rotation was held constant. Additionally, they found that the positioning of the observer's limbs during the task modulated parietal activity, likely due to the relationship between the observer's motor representation of their limbs and online proprioceptive feedback. Further, there is evidence that upper limb amputees show deficits in laterality judgment tasks (Nico et al., 2004). Though there is a great deal of support for Parsons model, it is not possible to know from the data provided whether motor representations are evoked as an obligatory part of the visual processing of a hand image, or whether these representations reflect contributions of the requirement to make an explicit laterality judgment.

Research into the nature of representations automatically evoked by a passively viewed static hand image is limited. To my knowledge there are three published studies addressing this topic. Each presents a series of hand-based SRC experiments, in which task-irrelevant hand images were presented in conjunction with a cue and participants made speeded two-choice keypress responses to discriminate some quality of the cue. Taken together, this literature has provided mixed results, and has produced conflicting accounts of the nature of visual hand representations. The topic is further obfuscated by differences and weaknesses in the methodologies employed in these past works.

The earliest account of hand-image based SRC effects was presented by Ottoboni and colleagues (2005). In their paradigm, participants completed two blocks of trials, in which they saw a brief (100 ms) display of a coloured dot superimposed on the image of a hand, which was cropped at the wrist (see Figure 1a). Participants made speeded keypress responses to the colour of the dot, with their hands in an uncrossed position on a keyboard. The view of the depicted hand (palm view or back view) was manipulated between blocks. SRC effects were not observed for either block of trials. In a second experiment, the stimuli were modified to include a portion of the forearm in the images. This modification was motivated by a study of explicit laterality judgment times, which reported longer response times (RTs) from participants who viewed only hands cropped at the wrist, compared to participants who viewed only hands with an attached forearm (Gentilucci et al., 2000). It is interesting to note, however, that the response time difference in the Gentilucci et al. study was not found to be statistically significant. Nevertheless, when forearms were added to the stimuli presented by Ottoboni et al., significant SRC effects emerged. Hands presented in back view produced positive compatibility effects, in that responses were made more quickly when the identity of the depicted hand matched the identity of the response hand (which also matched the location of the response key). Surprisingly, hands presented in palm view showed the reverse effect, in that responses were made more quickly when the identity of the depicted hand did not match the identity of the response hand. The authors proposed that this pattern of effects emerged because the forearm acted as an anchor, allowing the hand image to be mentally linked to an imaginary body. They suggested that the hand produced a spatial code based on its relative position on this imaginary body, from the observer's perspective. For example, when the back view of the hand with a forearm was shown, it was said to be linked to an imaginary body facing in the same direction as the observer, and thus the left hand of the body would occupy the same side of space as the observer's left hand – which produced, in their view, a left-sided extrinsic spatial code. When the palm side of the hand was shown with a forearm, they suggested that the imaginary body was facing toward the observer, and since the left hand of the imagined person would typically occupy the same side of space as the observer's right hand, it would have, in this view, generated a right-sided extrinsic spatial code. In other words, Ottoboni et al., claim that images of hands are represented in an extrinsic spatial manner, rather than being represented in terms of their identity as left or right hands in an effector-specific manner.

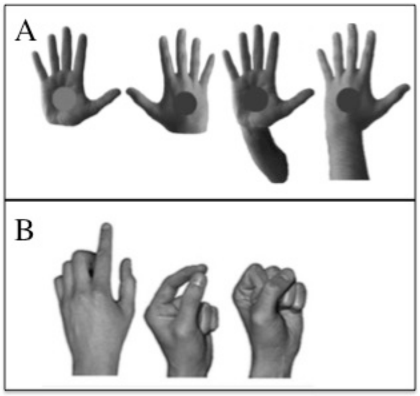

Figure 1. Sample stimulus images used in previous studies. Panel A depicts stimuli used by Ottoboni et al., (2005). Panel B depicts press, precision, and power postures used in Vainio and Mustonen (2011).

The claim by Ottoboni et al. (2005) that depicted limbs can generate correspondence effects consistent with the spatial location that the limb would typically occupy in observer-centric coordinates shares features of accounts of whole-body representations. For example, Taylor et al. (2016) proposed that depicted bodies automatically generate object-based spatial codes relative to the perspective of the observer. They found that when participants made keypress responses to the colour of an object held in the left or right hand of a figure facing either toward or away from the observer, faster responses were produced when the response location corresponded to the location of the object in an observer-centric frame of reference (e.g., a left response was compatible with an image of the figure facing toward the observer and holding a ball in its right hand on the left side of space). This effect persisted when the figure was rotated 90 degrees clockwise or counterclockwise and the cue locations were now aligned vertically, rather than horizontally. This indicated that the code generated by the cue was not linked to the left/right location of the cue on the screen (i.e., this was not a location-based Simon effect). Rather, the code seemed to correspond to the side of space that on which the cue would appear if the observed body were upright and aligned with the observer's body.

The conclusion presented by Taylor et al. (2016), like that proposed by Ottoboni et al. (2005), hinges on the assumption that effector-specific representations must inherently be view-independent. For example, since a palm view left-hand image (or a cue held in the left hand of a figure facing the observer) generated a code that corresponded to the observer's right hand, the authors assumed that that code could not correspond to a motor representation of the hand, because it does not follow a direct anatomical mapping (e.g., a left-hand image mapping to a left-hand representation). This assumption is challenged by the findings of Shmuelof and Zohary (2008), who report that viewing hand actions from an allocentric point of view activated visuomotor areas of anterior parietal cortex associated with the production of grasping actions, but in the hemisphere ipsilateral to the identity of the viewed hand. In comparison, viewing clips from an egocentric perspective was related to greater activity in the contralateral hemisphere, which was consistent with the pattern of activity generated by self-action. This finding suggests that when hand actions are viewed from an allocentric perspective, the observer's opposite identity hand is represented, but the nature of this representation is still visuomotor, and not merely an extrinsic abstract spatial representation.

If, based on the findings of Shmuelof and Zohary (2008), we can assume that allocentrically viewed hands, or palm-view hands, are capable of producing motoric, effector-specific, representations in a mirror like fashion, then it is possible that the SRC effects obtained by Ottoboni et al. (2005) are indeed effector-specific and grounded in motor representations. This leaves us with the question of why Ottoboni et al. obtained SRC effects only when they added a forearm to their hand images. Vainio and Mustonen (2011) made the argument that the very short presentation time of 100 ms utilized by Ottoboni et al. for both the hand prime and the response cue may have biased their results in two ways. First, SRC effects may have been disrupted because the hand stimulus was not displayed long enough and was removed from the display before response selection processes occurred. This disruption may have been even more significant for stimuli which were cropped at the wrist, as they contained less visual information about the laterality of the stimulus, and therefore it may have required a greater amount of time for the cropped hand images to evoke a laterality-based representation. Second, the effects may have been biased due to the simultaneous presentation of the prime hand and the colour cue. The time-course of SRC effects is sensitive to the extent of stimulus-onset asynchrony (SOA), the duration between the onset of the prime and the cue. For instance, the influence of the location of an object's handle on a keypress response was greater when a 1,200 ms delay occurred between the onset of the object image and the onset of the response cue, compared to when the object and cue were presented simultaneously (Phillips & Ward, 2002). Vainio and Mustonen suggested that the laterality of a task-irrelevant hand that is cropped at the wrist would be automatically encoded from a static image, if sufficient time were given for motor representations to build up prior to response and prior to the removal of the hand image from view.

Motivated by this hypothesis, Vainio and Mustonen (2011) conducted a series of experiments based on the SRC paradigm used by Ottoboni et al. (2005), with a few key modifications to the hand images, stimulus presentation durations, SOA, and the response cueing method. In their first experiment, hand primes were presented for 100, 400, or 700 ms prior to the onset of the task-relevant cue, which appeared for 200 ms while the hand remained on the screen for an additional 1,500 ms or until a response was made. The response cue was an image of an arrow oriented to the left or right, and participants were instructed to respond to a leftward-pointing arrow with a left keypress and a rightwardpointing arrow with a right keypress. There are potential ramifications of using a spatial cueing method in this paradigm, including potential issues surrounding a lack of ability to counterbalance response mappings, as well as the potential for stimulus-stimulus compatibility effects to develop, which I will discuss in more detail below. Three hand postures were shown: a power grasp, a precision grip, and a press posture (see Figure 1B). The authors proposed that these stimuli could be used to evaluate the claim made by Ottoboni et al. (2005) that the view of the hand (back or palm) would modulate hand-based correspondence effects, as one of their stimulus types clearly showed the back of a hand (the press posture), whereas the other two depicted a palm view of the hands (the precision-grip and the power-grasp postures). I would argue that the relationship between their stimuli and those used by Ottoboni et al. is not so clear cut, as the precision-grip posture image shows a side view of the hand with the wrist oriented vertically (perpendicular to the plane of the background). Additionally, hand images are complex stimuli and there are many differences between the depictions of each posture that extend beyond which side of the hand is visible. For example, the press and precision-grip postures both depict hands with quite significant visual asymmetries compared to the power-grasp hand. As well, with the precision-grip posture the thumb and forefinger appear to point to a side of space, which could provide a spatial cue. Nevertheless, the results of this experiment indicated that positive SRC effects were generated in response to all three hand postures. That is, participants were faster to produce a keypress response to the laterality of the arrow when it was superimposed on a hand of corresponding laterality.

Although hand posture did not modulate the direction of the hand-based correspondence effects in Vainio and Mustonen's (2011) experiment, posture did interact with the time course of the effect. For the power-grasp posture, the correspondence effect was present at the earliest SOA and remained relatively stable across the remaining two SOAs. However, SRC effects for the other two postures were not present at the shortest

SOA, but then grew rapidly across the time course, peaking at the 400 ms SOA with an effect size more than double the maximum effect size obtained with the power-grasp images. In a follow-up experiment, Vainio and Mustonen recreated the identical conditions of the first study, but presented the hand images rotated 180 degrees, so that the wrists were oriented toward the top of the screen (an allocentric viewpoint). Under these conditions, the SRC effects reversed, and participants were faster to respond to the arrow cue when the identity of the prime hand mismatched the identity of the response hand. The magnitude and time-course of the effects for each hand posture closely mirrored the pattern of results obtained with the egocentric hand stimuli, including the relationship between posture and SOA. Surprisingly, the authors did not propose a possible explanation for this most interesting interaction between posture and SOA, nor did they continue to use power-grasp posture images in their subsequent experiments to further explore this intriguing interaction. A later experiment using a single hand posture that depicted the palm surface of the hand and fingers replicated their general finding that egocentric hands (in which the wrists were aligned with bottom of the screen) generated positive SRC effects, while allocentric hands (in which the wrists were aligned with the top of the screen) generated reverse SRC effects. The author's main conclusion was that, contrary to Ottoboni and colleague's (2005) claims, disembodied hands are capable of generating correspondence effects, and both the palm and back view of the hand generate positive correspondence effects. Like Ottoboni et al., they claimed that when hand images depict an allocentric perspective, the hand image generates a code consistent with the viewer's hand of the opposite identity. Unlike Ottoboni et al., Vainio and Mustonen proposed that their effects, including the mirror-like effect in the allocentric condition, represent the contribution of effector-specific motor codes, rather than extrinsic spatial codes.

To investigate their hypothesis that hand images evoke effector-specific motor representations, Vainio and Mustonen (2011) conducted a further experiment in which participants made keypress responses to arrow cues with the index and middle finger of one hand, rather than the index fingers of two hands. A single SOA of 600 ms was used in this experiment and two different hand postures were shown: the precision grip from the first experiment, and a new image depicting the back of a hand with the thumb, index, and middle finger outstretched, made to replicate the hand posture adopted by the participants during the study. Overall, SRC effects were not produced under these conditions. There was a tendency for right finger responses to be faster for right-hand stimuli as compared to left-hand stimuli, but opposite pattern was not found for left finger responses. Further, the interaction between response finger and depicted hand laterality was not significant. This null result served as the primary evidence presented by Vainio and Mustonen in favour of their proposal that hand images trigger effector-specific motor representations. The methodology used in this study, as well as the way in which the authors interpreted their results, fits with the conventional understanding regarding a within-hand response arrangement in an SRC paradigm. Namely, a null result generated in the context of a within-hand response mode is taken as positive evidence of an effector-specific representation. This interpretation is predicated on the assumption that if a spatial code were generated under these task conditions, then a significant SRC effect would emerge due to the spatial locations of the response keys. However, recent work has challenged the assertion that within-hand response arrangements are suitable for testing whether motor representations contribute to SRC effects (for a recent discussion see Bub et al., 2021). Moreover, the null effect in this study was established using null-hypothesis significance testing which does not allow one to draw conclusions about the degree of support seen in favour of the null hypothesis. Given the small sample size used in this experiment (n = 12), a null effect might simply reflect insufficient power to detect an effect. A more convincing arrangement to test the relative contributions of effector-specific and extrinsic spatial codes would be to have participants respond under crossed-hand conditions, as Wallace (1971) did to demonstrate that the classic Simon-effect is generated by extrinsic spatial codes.

As previously mentioned, another feature of the method employed by Vainio and Mustonen (2011) was potentially problematic for the interpretation of their results. In the studies described above, participants responded to the direction of an arrow cue superimposed on a hand image, rather than to the colour of a dot like that used in Ottoboni et al. (2005). This cuing method is questionable because unlike a coloured dot, an arrow has an inherent spatial component. Consider for instance the difference between an image of a left hand with a blue dot superimposed on it and an image of a left hand with a right arrow superimposed on it. The stimulus with the blue dot carries no inherent spatial information beyond what may be provided by the hand. Until this image is presented in a task context in which the colour blue has been mapped to a particular response, there is no opportunity for a compatibility effect to arise. However, the same hand image with a right arrow replacing the dot can generate two codes (one associated with the hand and one with the arrow), which may be compatible or incompatible, and this compatibility can be determined even in the absence of task-based stimulus-response mapping instructions. This type of compatibility is referred to as stimulus-stimulus (SS) compatibility, and SS compatibility effects have been found to be additive with SRC effects (e.g., Kornblum, 1994). This is especially concerning as it applies to Vainio and Mustonen's paradigm, given that SS and SR compatibility are not independent in their experimental design. Any stimulus that is SS compatible will also be SR compatible and any SS incompatible stimulus will also be SR incompatible, since the relationship between the response and the direction that the arrow is pointing is fixed throughout the study. In order to understand the nature of hand representations automatically evoked by a depicted hand, it is essential to understand whether the hand image produces a code that corresponds to or conflicts with a response code – which cannot be determined from Vainio and Mustonen's results due to their use of a spatial cuing stimulus.

Given the methodological issues associated with the work by both Ottoboni et al. (2005) and Vainio and Mustonen (2011), no definitive conclusions can be drawn from these studies regarding the nature of representations automatically evoked by a static hand image. In the present thesis, I aimed to develop a methodology to assess the nature of SRC effects generated by task-irrelevant hand images. I began by creating a standard methodology that aimed to address the disadvantages of the previous work that seemed the most likely to have obfuscated past results. Like Ottoboni et al., I used a coloured dot to cue responses based on an arbitrary response-key mapping that was counterbalanced between participants. In this way, I avoided the potential SS compatibility confound that is present in Vainio and Mustonen's experiments. Like Vainio and Mustonen, I presented the stimuli with various SOA durations (100 and 500 ms). In this way I avoided the potential pitfalls of Ottoboni's brief and simultaneous stimulus presentation method. In my method, both the prime and the cue remained on screen until a response was made, to avoid any potential drawbacks of removing the cue prior to response that may have been present in Vainio and Mustonen's experiments. I piloted my method by testing whether SRC effects are modulated by the presence/absence of a forearm (as theorized by Ottoboni et al.). This pilot testing revealed significant SRC effects overall. The effect sizes I obtained were very small (approx. 15 ms), which led me to increase the target sample size for the experiments presented in this thesis from 32 to 48 (though note that this sample size was then increased further for studies that were run online due to the impact of the COVID-19 pandemic on in-person data collection). Additionally, this pilot testing revealed that the forearm did not significantly modulate the SRC effects produced in my paradigm, which allowed me to move forward using only images of hands that have been cropped at the wrist.

In this thesis I present a series of five experiments, each of which has been designed to contribute to our understanding of the nature of representations automatically evoked by a hand image. These experiments will provide support for the following claims: 1) static images of hands can generate SRC effects that are modulated by the viewpoint (egocentric or allocentric) of the hand; 2) these SRC effects are effector-specific and likely reflect contributions made by motor representations during visual processing; 3) the nature of the representation evoked by the image of a hand can be shifted from an effector-specific code to an extrinsic spatial code merely by changing the visual properties of that hand image; 4) hand images that typically evoke extrinsic spatial codes can be made to evoke effector-specific codes by changing the demands of the task; 5) task-irrelevant hand images that evoke effector-specific SRC effects do not influence the coding of a handled object on which they are superimposed, in the absence of a laterality judgment task. Together, these experiments show that the nature of the representation evoked by a depicted hand is determined both by task demands and by the visuospatial properties of the depicted hand posture.

Experiment 1

Introduction

The primary aim of Experiment 1 was to investigate whether the viewpoint from which a task-irrelevant hand image was presented (egocentric or allocentric) modulates SRC effects- as well as to collect preliminary evidence regarding whether such SRC effects reflect contributions of extrinsic spatial or effector-specific representations of the depicted hand.

Participants in this experiment viewed images of hands in a power-grasp posture (see Figure 2). Selection of a power-grasp posture was advantageous in that by depicting the hand with the fingers clenched, there was a reduced possibility that the fingers would draw the observers attention to a particular part of the hand (in contrast to, for example, a press-posture in which an outstretched index finger and thumb might draw attention to one side of the hand) or to a particular side of space (in contrast to, for example, a precision-grip posture, in which the outstretched fingers might appear to point away from the hand and draw attention to the side of space to which the fingers are pointing). The power-grasp hand images were presented from an egocentric (Experiment 1a) or allocentric (Experiment 1b) viewpoint. Both viewpoints showed the identical hand image, differing only in the degree to which the image was rotated (0 or 180 degrees). After either a 100 or 500 ms presentation of the hand image, a coloured dot was superimposed on to the hand. Participants made speeded keypress responses to the colour of the dot, and – depending on the experimental block – made their responses with their hands either in a crossed or an uncrossed position. SRC effects were examined based on an anatomical coding of compatibility. That is, a trial was coded as *compatible* when the laterality of the depicted hand matched the laterality of the hand used to make a correct response on that trial, regardless of whether the correct response involved depressing a left or right-sided response key. This method of coding on the basis of anatomical compatibility, rather than spatial compatibility, is maintained throughout the thesis wherever it is applicable.

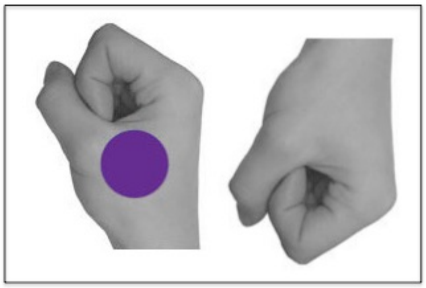

Figure 2. Sample images of hands in a power-grasp posture. On the left, a sample image of an egocentric right hand with the colour dot cue present. On the right, an allocentric left-hand image without the colour cue.

I made two specific predictions regarding the outcomes of Experiment 1. First, I predicted that for both response modes in Experiment 1, SRC effects would emerge and the direction of the SRC effect would remain consistent across response modes. A result consistent with this prediction would imply that the selection of the response hand is responsible for generating the SRC effect, rather than the spatial location of the response key. Such a finding would suggest that the hand images evoke an effector-specific representation and are automatically coded according to an intrinsic frame of reference. Neuroimaging work by Shmuelof and Zohary (2008) demonstrated that in the context of viewing object-directed hand actions motor-like activation could occur in either a direct fashion (e.g., a left-hand image evokes a left-hand representation) or, in the case of allocentrically presented stimuli, in a mirror-like fashion (e.g., a left-hand image evokes a right-hand representation). Based on this result, as well as on work by Vainio and Mustonen (2011), my second prediction was that hands presented egocentrically (Experiment 1a) would generate a positive SRC effect, whereas hands presented allocentrically (Experiment 1b) would generate a negative SRC effect. These predictions were generally supported by the data.

Method

Participants. Participants in Experiments 1a and 1b were recruited from a pool of undergraduate students at the University of Victoria, who participated for extra credit in a psychology course. Each participant participated in only one experiment presented in this dissertation. The University of Victoria Human Research Ethics Board approved the protocol for these experiments.

In expectation of a small effect size based on my pilot data, I set an a priori target sample size of 48 participants for each experiment. Previous studies in our lab suggested that this sample size would be adequate for detecting small effect sizes using Bayesian analyses. I also established a priori a protocol to exclude any participant who obtained less than 80% task accuracy. All participants reached this accuracy threshold in Experiment 1. Of the 96 participants included in Experiments 1a and 1b, 73 were female, 86 were right-handed, and the median age was 20 yr (range 18 to 42 yr).

Materials. A greyscale photograph of a hand in a power-grasp posture was taken from an overhead position (see Figure 2). Two versions of each photograph were generated, such that the opposite laterality version of the stimulus was a mirror reversal of the original image. The dimensions of these hands were approximately 130 x 175 pixels, and they were placed on a white background of 200 x 200 pixels. Image versions that included the coloured dot were created by placing a coloured dot of approximately 50 pixels in diameter near the middle of the hand image. This placement allowed for an unobstructed view of all fingers. The two dot colours were each paired with the two hand images. Images in Experiment 1a were presented from the egocentric view (the wrist was aligned with the bottom of the screen). In Experiment 1b, these images were rotated 180 degrees to present an allocentric view of the hands.

Procedure. Participants were tested individually in a quiet room under the supervision of an experimenter. They sat at a desk with a computer monitor positioned approximately 50 cm away. A response box with a row of seven response keys was placed on the desk immediately in front of the participant within easy reach and approximately aligned with the center of the monitor and the participant's midline. The distance between the centers of the outermost keys was approximately 16.5 cm. Presentation of stimuli on a monitor and collection of response data were controlled by an iMac computer.

Participants were informed that they would see a picture of a hand, which was not relevant to their task, followed by a coloured dot, and that their task was to respond to the colour of the dot by making a keypress. Participants completed two blocks of trials. In one block, participants used their left index finger to press the left-most response key, and their right index finger to press the right-most response key (straight-hand response mode). In the other block, participants crossed their arms and used their left index finger to press the right-most key, and their right index finger to press the left-most key (crossed-hand response mode). The order in which these blocks occurred was counterbalanced across participants. Participants were instructed to press the left key if the dot was one particular colour and the right key if it was the other colour. One set of colours was used in each block (blue/green or orange/purple) to ensure that the colour to key assignment in the first block did not interfere with performance in the second block. Colour-pair-to-block and colour-to-key assignment was counterbalanced across participants. Participants were instructed to make their responses as quickly and accurately as possible. Compatibility was defined as a match between the laterality of the depicted hand and the laterality of the response hand on correct trials.

Each trial began with the presentation of a fixation cross at the center of the monitor for 250 ms. The screen was then blank for 250 ms before the image of a hand appeared. The coloured dot was superimposed on the hand after either a 100-ms or 500-ms delay. The hand and dot ensemble remained in view until the participant made a keypress response. If the response was incorrect the word *error* was immediately displayed on the screen for 1,000 ms. Following an intertrial-interval of 750 ms the next trial began.

Each block of trials began with 16 practice trials, followed by 160 critical trials. Across the critical trials, each of the hand/dot pairings at either SOA was shown 20 times in a random order, for a total of 320 critical trials. A self-regulated rest break was provided after every 40 critical trials.

Results

Across both versions of Experiment 1, the mean accuracy on the colour judgment task was 97.5%, and participant accuracy ranged from 85-100%. Response time was defined for each trial as the time between the onset of the coloured dot and the keypress response. Response times less than 100 ms were considered anticipatory, and faster than the minimum plausible response and were therefore excluded from analysis. Additionally, an upper bound on response times was then set for each version of the experiment so that no more than 0.5% of the total correct responses were excluded

(Ulrich & Miller, 1994). This exclusion criterion was applied to all experiments reported here, leading to some variation in the upper bound value. Following this guide, Experiments 1a and 1b this upper bound was set at 1,100 ms and 1,000 ms, respectively. Incorrect trials were also removed from the response time analyses.

Stimulus-response compatibility effects were assessed by computing Bayes factors using the *anova*BF function in the *BayesFactor* package in **R** (Rouder, et al., 2017). The default priors in this package for the alternative hypothesis in factorial designs were used. I specified 100,000 iterations for convergence and selected the *whichModels="top"* option – which involved comparing a model that includes all of the effects in the design against a model that excludes a specific effect, with each effect considered in turn. If a model including the effect is favoured, it is considered evidence in support of that effect. If the model excluding the effect is preferred, that is taken as support in favour of the null effect. This analysis produces a Bayes factor (*BF*) for each effect, supporting either its presence or absence. Bayes factors of 3 or greater are generally taken as positive evidence for the favoured model and a Bayes factor greater than 20 is considered to be "strong" evidence (Raftery, 1995). An important caveat to using this procedure is that the *anovaBF* function is based on a model that assumes the sphericity assumption has been met. That is, for repeated-measures factors, all conditions have equal population variance and there is equal covariance for all pairs of conditions. When this assumption is violated, the Bayesian model may not be able to accurately assess the influence of the variables of interest. My approach to data analysis was therefore to first assess whether the sphericity assumption was met by the given data set by treating the full set of conditions as discrete levels of a single factor in an analysis of variance using the *ezANOVA* function in the *ez* package in **R**. If a Huynh-Felt ε value of less than 0.75 was obtained, then I moved to estimate the Bayes factors using the Bayesian information criterion (BIC) as described in Wagenmakers, 2007 (see Masson, 2011, for a description of the procedure used in the analyses reported here). This BIC approximation of the Bayes factor is considered to be a relatively conservative test in regard to finding support in favour of the alternative hypothesis (Raftery, 1999).

The error bars presented with response time and percent error condition means in the Figures are 95% highest-density intervals (HDIs) for repeated-measures comparisons computed using the *rmBayes* package in **R**. The error bars presented with the quintile means in the delta plots represent 95% HDIs for the compatibility effects, generated using the *ttestBF* and *HPDinterval* functions in the *BayesFactor* package in **R** with the default prior distribution.

Experiment 1a results

Response time. For egocentrically presented hand images, an analysis was conducted including response mode (straight or crossed hands), SOA, and anatomical compatibility as factors. Anatomical compatibility was defined as a match between the laterality of the depicted hand and the laterality of the response hand. For example, a left-hand image was compatible with a left-hand/left-key response in the straight-hands response mode, and a left-hand/right-key response in the crossed-hands response mode. The mean RTs for each condition are presented along with percent error in Figure 3.

For the response time data, the sphericity assumption was not met ($\varepsilon = 0.60$). A BIC approximation procedure was used to generate an estimate of the Bayes factor for the main effects and interactions in the full analysis of the data. There was very strong evidence of a main effect for all three factors in the analysis. Responses made with straight hands were faster (421 ms) than with those made with crossed hands (449 ms; *BF* = 708.1). The slowing of keypress responses under crossed-hand response conditions compared to straight-hand response conditions is a standard finding in stimulus-response compatibility studies, and not of particular interest here. Responses were made more quickly at the longer SOA than the shorter SOA (414 ms vs. 456 ms; *BF* > 1,000), which is also a standard general finding in these types of paradigms. Critically, responses times when the laterality of the response hand and the depicted hand matched were shorter (430 ms) than responses made when the response and hand depicted hand did not match (441 ms; *BF* > 1,000). Evidence for all other interactions favoured the null model over the alternative by a Bayes factor of at least 2. Importantly, this includes a null interaction between anatomical compatibility effect and response mode (*BF* = 6.7). The SRC was positive under both straight- and crossed-hand conditions (mean effect size =11 ms and 12 ms, respectively). This result is consistent with the hypothesis that the hand image is coded according to an intrinsic/anatomical frame of reference, and the hand therefore evoked an effector-specific representation, rather than an extrinsic spatial code.

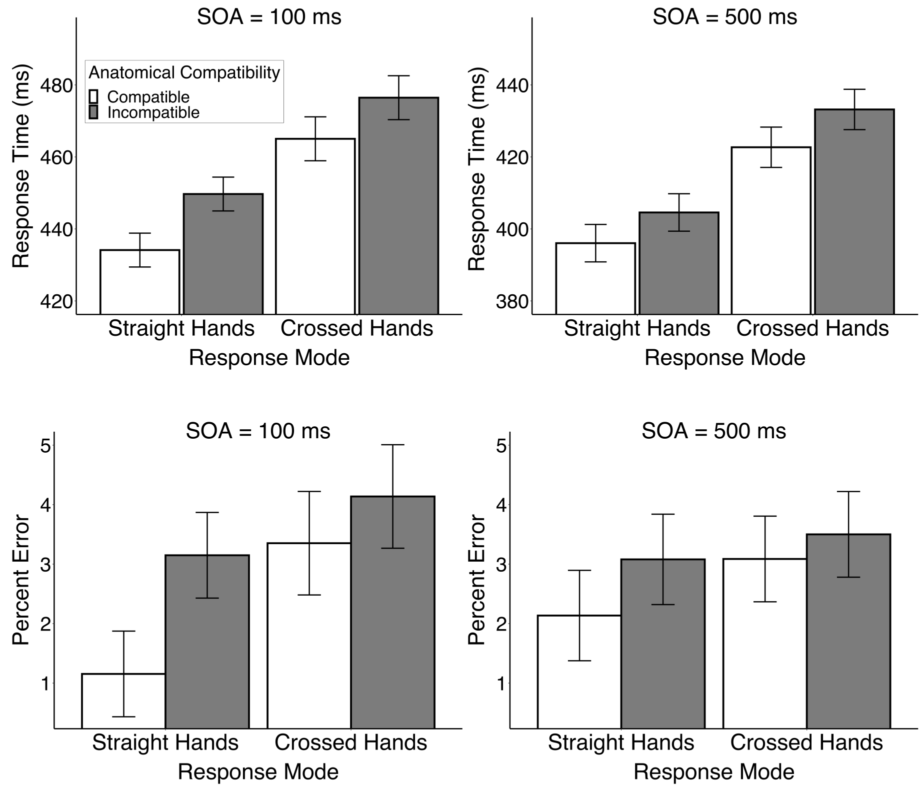

Figure 3. Mean response time and percent error in Experiment 1a as a function of SOA, response mode, and anatomical compatibility. Note that the range of response times is different for the two SOA conditions

Percent error. The percent error data were analyzed in the same fashion as the response time data. For these data, the sphericity assumption was met (ε = .76), and a Bayesian analysis found strong evidence for a main effect of anatomical compatibility (BF = 52.6). Fewer errors were made when the correct response hand was anatomically compatible with the depicted hand, compared to when they were incompatible (2.4% vs. 3.5%). There were also fewer errors in the straight-hands condition than the crossed-hands condition (2.4% vs. 3.5%; BF = 186.2). Evidence for the main effect of SOA as well as any interactions favoured the null by a Bayes factor of at least 2.

Response time distribution. The time course of the anatomical compatibility effect was examined further by way of a quintile analysis and the construction of delta plots (Pratte, et al., 2010; Ridderinkhof, 2002). Five quintiles were constructed by rank ordering the trials of each participant for each of the anatomical compatibility and response mode conditions by response time. An equal number of trials were then distributed into each quintile, such that the first quintile contained the 20% of trials with the shortest RT, and next 20% shortest were placed in the second quintile, and so on. In cases in which the number of correct trials for a given participant and condition was not divisible by 5, the additional observations were included in quintile bins in descending order. The mean response time in each quintile for each anatomical compatibility and response mode condition was used to compute the compatibility effect size for each participant for each quintile, by response type and SOA. The mean anatomical compatibility effect by response type across quintiles is shown as a delta plot in Figure 4.

A linear trend analysis was applied to assess the slope of each delta plot across quintiles. For each participant, the compatibility effects across quintiles were multiplied by a set of weights representing a linear trend (-2, -1, 0, 1, 2). The mean weighted sums across the sample were tested against a null hypothesis with a value of zero, using the *ttestBF* function in the *BayesFactor* package in **R** with the default prior distribution. There was moderate evidence that the response time distribution for straight-hand responses at the short SOA follows a linear trend, with the mean weighted sum of effect sizes equal to 11 ms, which is reliably different from zero ($BF = 6.6$). For straight-hand responses made at the longer SOA, as well as crossed-hand responses at the short and long SOAs the weighted sums (-2.7 ms, 5.6 ms, and 2.8 ms) were not reliably different from zero ($BF = 5.0$, 2.9, and 5.4, respectively), which implies that the compatibility effect was flat across the response time distribution in these conditions.

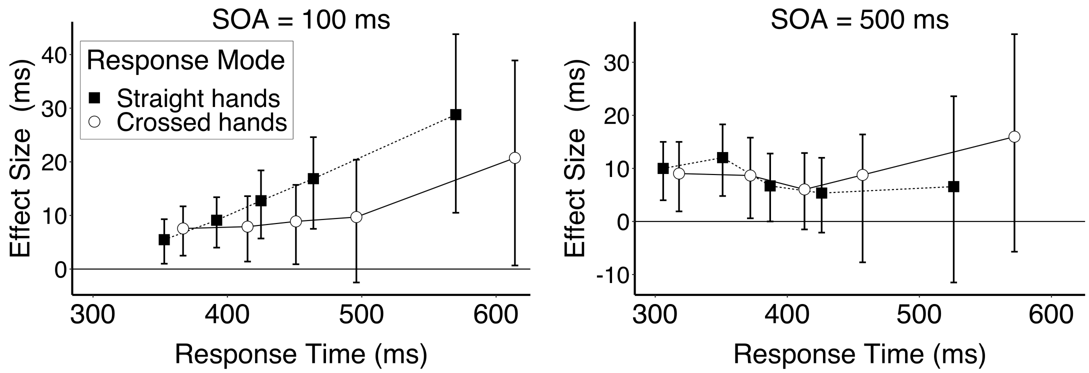

Figure 4. Response time delta plot for the anatomical compatibility effect in Experiment 1a. Response time refers to the mean response time at a specific quintile, averaged across compatible and incompatible conditions.

Experiment 1b results

Response time. For allocentrically presented hand images, an analysis was conducted with the factors of response mode, SOA, and anatomical compatibility. The mean RTs for each condition are presented along with percent error in Figure 5. The sphericity assumption was not met by the response time data (ε = 0.39). The BIC approximation of the Bayes factor indicated very strong evidence of a main effect of response mode (*BF* > 1,000) and SOA (*BF* > 1,000). Both of these main effects followed the expected trend based on the results of Experiment 1a. That is, responses were made more quickly with straight hands compared to crossed hands, and responses were made more quickly at the longer SOA compared to the shorter SOA. The mean RTs trended in the negative direction (compatible = 426 ms, incompatible = 422 ms), which is consistent with my prediction that allocentrically presented hands would be coded in a mirror-like fashion (i.e., left hand responses would be faster when primed by an allocentric right hand). However, evidence for the main effect of anatomical compatibility only anecdotally favoured the alternative model (*BF* = 1.8). Evidence for all interactions favoured the null model by a Bayes factor of at least 6, with the exception of the interaction between compatibility and SOA, which only anecdotally favoured the null (*BF* = 1.9). Given this inconclusive finding, as well as the visual differences in the magnitude of the compatibility effect across SOA seen in Figure 5, I conducted separate analyses for each SOA. When the analysis was restricted to the short SOA, I obtained positive evidence in favour of an effect of compatibility (*BF* = 15.8), which crucially did not interact with response mode (*BF* = 6.9). When the analysis was restricted to trials with a long SOA, the evidence favoured the null interpretation of the main effect of compatibility, as well as the compatibility by response mode interactions (*BFs* = 6.0 and 6.9, respectively). Although not as conclusive as the response time results seen in Experiment 1a, these findings do weakly suggest that hand images presented allocentrically generate effector-specific representations of the viewer's opposite-laterality hand.

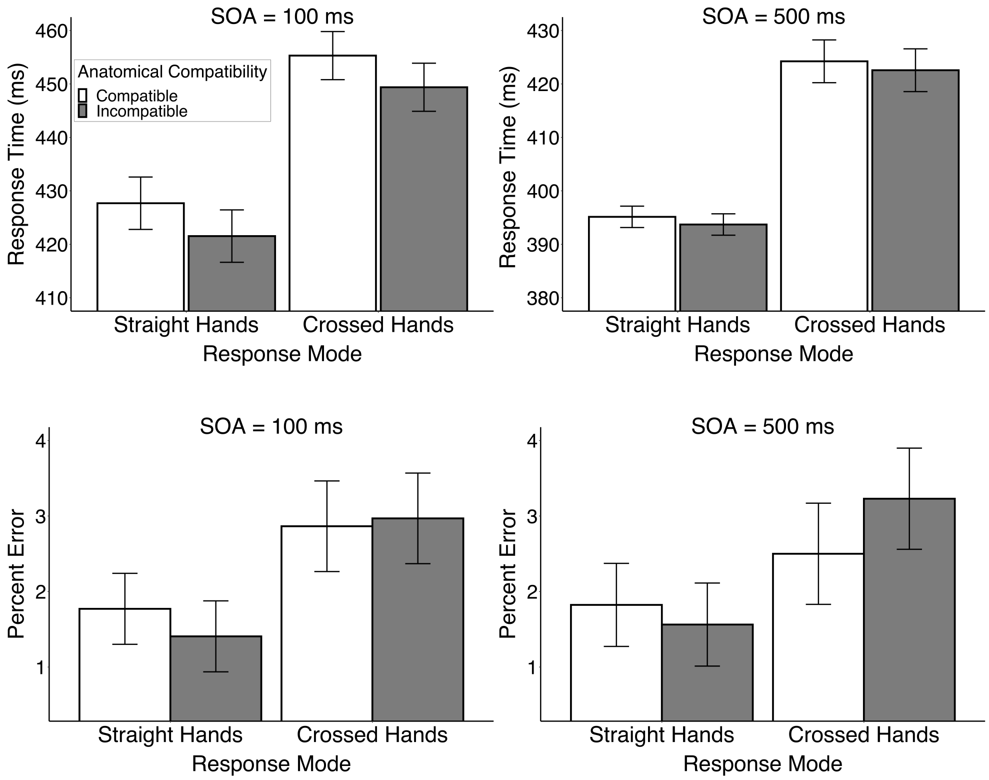

Figure 5. Mean response time and percent error in Experiment 1b as a function of stimulus onset asynchrony (SOA), response mode, and compatibility between the laterality of the hand cue and the identity of the correct response hand.

Percent error. For the percent error data, the sphericity assumption was met (ε = .77) and a Bayesian analysis produced evidence in favour of only the main effect of response mode (*BF* > 1,000). There were fewer errors in the straight-hands condition than the crossed-hands condition (1.6% vs. 2.9%). All other main effect and interactions generated a Bayes factor of at least 3 in favour of the null, except for the interaction between response mode and anatomical compatibility, which produced a Bayes factor of only 1.7 in favour of the null. When each response mode was analyzed separately all main effects and interactions favoured the null for both response modes by a factor of at least 3.

Response time distribution. Delta plots were constructed using the same method described for Experiment 1a. The mean anatomical compatibility effect size for each condition across the response time distribution can be seen in Figure 6. Linear trend analyses for these data suggest support an interpretation of a flat delta plot for all conditions. The mean weighted sum and Bayes factor results for each condition are presented in Table 1.

Table 1. Results of linear trend analyses for Experiment 1b.

Response mode	SOA	Mean weighted sum	Bayes Factor
Straight hands	100 ms	-5 ms	2.1 in favour of null
Straight hands	500 ms	5 ms	2.5 in favour of null
Crossed hands	100 ms	-1.2 ms	6.0 in favour of null
Crossed hands	500 ms	0 ms	6.4 in favour of null

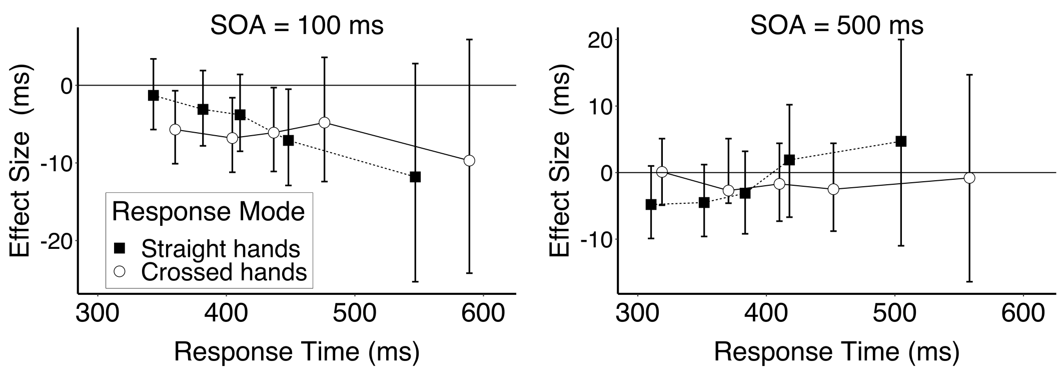

Figure 6. Response time delta plot for the anatomical compatibility effect in Experiment 1b.

Discussion

Experiment 1a established that power-grasp images presented from an egocentric viewpoint generate an SRC effect when participants make speeded left/right keypress responses to the colour of a cue superimposed on the hand images. This SRC effect was positive, meaning that compatibility between the depicted and response hands was associated with faster responses compared to when the stimulus and response hands were incompatible. Critically, response mode (straight or crossed hands) did not modulate the SRC effect. This finding suggests that in the context of this paradigm, responses are coded in terms of left/right response hand, rather than left/right response key. This provides evidence in support of the hypothesis that unlike stimuli typically used in SRC paradigms (arrows, spatially displaced dots, etc.), images of power-grasp hands are coded according to an intrinsic frame of reference, even when the hands are task-irrelevant.

The magnitude of the SRC effect generated by egocentric power-grasp hands remained fairly consistent across SOAs, which is consistent with the relatively flat effect observed by Vainio and Mustonen (2011) on power-grasp trials across 100, 400, and 700 ms SOAs. The delta plot reveals that under both response modes the SRC effect is present for even the fastest responses, which indicates that the laterality of the hand image is rapidly processed. For responses made with straight hands the delta function grows linearly across the response time distribution, which is a typical finding for Simon-like tasks in which the cue is presented centrally (see Proctor, et al., 2011 for a review). An increasing function might suggest that the effect grows as stimulus presentation time grows, or as response selection time increases. Here, the effect size reaches an asymptote and is flat at the longer SOA, which suggests that the effect builds in magnitude with increased stimulus presentation time – which may reflect the time course of the extraction of laterality from the depicted hand image. Compared to straight-hand responses, response time (and, hence, stimulus viewing time) is greater at each quintile for crossed hands, which provides a possible account of why only flat functions are obtained under the crossed-hands response conditions.

As predicted, when hands were presented allocentrically (Experiment 1b), the mean response time was shorter when the depicted hand and the response hand were incompatible, compared to when they were compatible. In line with the evidence presented by Shmuelof and Zohary (2008), this suggests that allocentric hand images can evoke a representation of the observer's own hand, in a mirrored fashion (e.g., an allocentric left hand is mapped to the observer's right hand). However, in contrast to the effects produced by egocentric hands, this finding was less robust – with the Bayesian analysis providing only anecdotal support in favour of the presence of an effect of anatomical compatibility across both SOAs. In a standard factorial ANOVA of the full data set, the main effect of anatomical compatibility meets the standards of null hypothesis significance testing to reject the null, $F(1, 47) = 5.2$, $p = .027$. This might indicate that the failure to replicate the clear reverse compatibility effect with allocentrically presented hands reported by Vainio and Mustonen (2011) was due to the relatively conservative nature of the BIC approximation of the Bayes Factor, compared to NHST analyses.

Further, the relative weakness of the SRC effect in Experiment 1b might reflect differences in the time course of the effect. When separate analyses were conducted for each SOA, a clear SRC effect was present at the short SOA, but no such effect was found at the longer SOA. The apparent reduction of this effect was equivalent for both response modes, which suggests that it reflects a rapid decaying of the effector-based SRC, rather than contributions of an increasing spatially based effect, which would create an apparently diminishing effect under one response mode (when spatial and effector based codes conflicted) but a growing effect under the other response mode (where the effects would be additive).

Given the less robust nature of the SRC effect in Experiment 1b, I opted not to further pursue questions about allocentrically presented hands. All subsequent experiments use solely hand images presented egocentrically (though note that work by Ottoboni et al., 2005, refers to hands in palm view as being allocentric, whereas for the purposes of this thesis palm-view hands are considered to be egocentric).

Experiment 2

Introduction

Experiment 1 provided evidence that passively viewed egocentric power-grasp primes provide a response time advantage for responses made with the observer's matching hand, regardless of the location (left or right) of the response key. To follow up these results, I conducted two further studies using the same experimental stimuli and design, but introduced two different response modes. In Experiment 2a participants responded in one block of trials using the middle and index finger of their dominant hand, and in another block of trials using the index fingers of both of their hands. In Experiment 2b participants responded using the index fingers of both hands on vertically oriented keys.

The benefit of conducting these follow-up studies was threefold. First, replicating the results of the straight-hand response mode block in Experiment 1a with the identical between-hands response mode block in Experiment 2a allowed me to establish that the SRC effects generated using this paradigm are reliable and robust. Second, as effector-specific codes are relatively uncommon in the SRC literature, this gave me the opportunity to further probe the appropriateness of using a within-hand response mode design to distinguish between effector-specific and spatial effects. Comparisons of within-hand and between-hand response modes to differentiate between extrinsic spatial and effector-specific accounts are rather pervasive in the literature despite potential theoretical problems with using these methods. I discussed earlier one such limitation of these comparisons, that the absence of a within-hand SRC effect does not necessarily indicate the presence of an effector-specific representation. A potentially even more challenging suggestion is that motor-based representations might be capable of producing within-hand SRC effects due to dimensional overlap between an element of an effector-based response and a key-based response (Kornblum, et al., 1990). Just as people are quite capable of mapping 1, 2, and 3, to *a, b,* and *c,* it is possible that motor codes may be translated into spatial codes under particular task conditions (e.g., a left-hand representation might be mapped to a responding forefinger, if that is the left-most response option). To my knowledge, evidence that such a translation might occur is limited to a single finding, in which a SRC effect was found in a within-hand response mode for an effect that was previously found to be effector-specific in nature (Ullrich, unpublished thesis). Though the results I obtained using a within-hand response mode did not replicate that finding, the relatively weak evidence obtained by comparing results from within-hand and between-hands response modes suggests that use of a crossed-hand response mode, not a within-hand response mode, should be the standard when distinguishing between effector-based and spatial SRC effects.

The third benefit to modifying response mode in these follow-up experiments was to attempt to ascertain a potential influence of task context on the SRC effects. The results of Experiment 1 suggested that SRC effects are generated due to the activation of an effector-specific representation of a depicted hand. I make the claim that this representation is evoked automatically as the hand image is task-irrelevant. However, it is important to acknowledge that any effect of "automatic" processing of the hand's laterality might occur only due to the context of the task requiring a lateralized response. Of course, it is not possible to measure hand-based SRC effects without the use of a task that requires a response. However, I can try to limit one possible way in which task demands might contribute to SRC effects. Experiment 2b was designed in an attempt to eliminate the possibility that the laterality of the depicted hand was processed only due to the spatially lateralized nature of the responses. In other words, was the left/right identity of the hand extracted due to the requirement that participants make left/right spatial response? By arranging response hands in a vertical alignment, this left/right-lateralized element of the task was removed, which did not seem to influence the presence of the SRC effect.

Method

Participants. In each of Experiments 2a and 2b, 48 students who had not participated in another version of this experiment were recruited from the same participant pool used in Experiment 1. All participants met the threshold of 80% task accuracy and were included in the analysis. Of the 96 participants across both versions of the experiment, 76 were female, 93 were right-handed, and the median age of the participants was 20 yr (range 18 to 41 yr).

Materials. Power-grasp hand images were presented from the egocentric viewpoint only. The stimuli used were the same as those presented in Experiment 1a.

Procedure. The procedure was identical to Experiment 1, except for the response mode used in each version of the experiment. In Experiment 2a, participants completed one block of trials using a within-hand response mode, in which they made their responses using the middle and index finger of their dominant hand on response keys that were immediately adjacent to one another (approximately 3-cm distance between the centers of the response keys; see Figure 7). In the other block of trials responses were made between hands, in the standard straight-hand response mode described in Experiment 1. In Experiment 2b, the response box was rotated 90 degrees, so that the keys were aligned along the vertical, rather than horizontal dimension (see Figure 7). Participants completed one block of trials in which they responded with their left index finger on the top-most button and their right index finger on the bottom-most button, and one block of trials in the opposite configuration. Block order was counterbalanced between participants. All other elements of the experimental design in Experiment 2 were identical to Experiment 1.

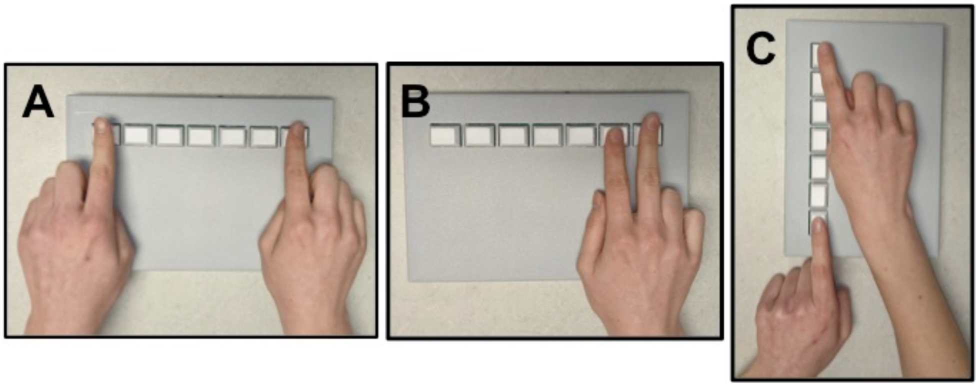

Figure 7. Demonstration of the response box set up for between-, within-, and vertical-hand response modes (Panels A, B, and C, respectively).

Results

Averaging across both versions of Experiment 2, mean accuracy on the colour dot task was 98.4 %, and ranged from 94-100% correct. Following the outlier removal procedure described in Experiment 1, response times less than 100 ms or greater than 1,000 ms were excluded for both Experiment 2a and 2b. Incorrect trials were also removed from the response time analysis.

Experiment 2a results

Response time. An analysis was conducted with the within-subject factors of response mode, SOA, and spatial compatibility. As anatomical compatibility could not vary in the within-hand response mode, spatial compatibility was used as a factor in this experiment, defined as a match between the laterality of the depicted hand and the spatial location of the response key relative to the incorrect key. Note that since between-hand responses were made with straight hands, for this response mode the concept of spatial compatibility is interchangeable with anatomical compatibility. Mean correct response time and percent error as a function of spatial compatibility, SOA, and response mode are shown in Figure 8.

For the response time measure, the sphericity assumption was not met ($\varepsilon = 0.38$), and I therefore computed an approximation of the Bayes factor using by utilizing the BIC. Evidence in support of a main effect of response mode was merely anecdotal (*BF* = 1.3). The mean response time for responses made between two hands (411 ms) was shorter than responses made within one hand (421 ms). A main effect of SOA in the expected direction was strongly supported (*BF* > 1,000). There was also positive evidence of a main effect of spatial compatibility (*BF* = 16.7). Evidence for the response mode by spatial compatibility interaction did not favour either the null or alternative model (*BF* = 1.0). The 3-way interaction between response mode, spatial compatibility, and SOA only anecdotally favoured the alternative (*BF* = 1.2).

When effects at each SOA were assessed independently, responses made on short SOA trials showed strong evidence of an effect of spatial compatibility (*BF* > 1000), while there was not support for a main effect of response mode (*BF* = 1.6 in favour of the null). Critically, there was strong evidence for an interaction between response mode and spatial compatibility (*BF* = 20.7). For responses made with two hands at the short SOA, there was very strong evidence in favour of the compatibility effect (*BF* > 1000), with compatible responses made on average 14 ms faster than incompatible responses. For responses made with one hand at the short SOA the null model was favoured (*BF* = 2.3). Responses made at the long SOA showed anecdotal evidence in support of a response mode main effect (*BF* = 1.9), but provided no evidence in favour of a spatial compatibility effect (*BF* = 2.7), nor of a compatibility by response mode interaction (*BF* = 6.9).

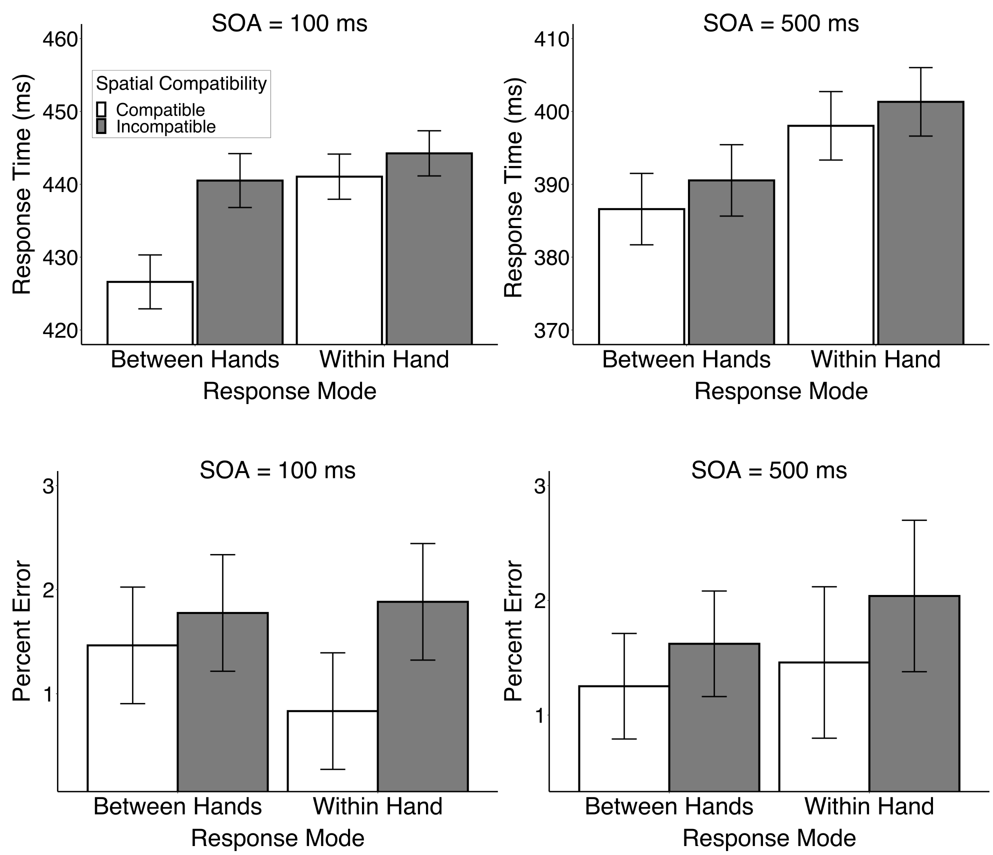

Figure 8. Mean response time and percent error in Experiment 2a as a function of stimulus onset asynchrony (SOA), response mode, and compatibility between the laterality of the hand cue and the spatial location of the correct response key.

Percent error. For the percent error data, the sphericity assumption was met (ε = .77). A Bayesian analysis revealed a main effect of spatial compatibility (*BF* = 7.4), in which fewer errors were made under compatible conditions than incompatible (1.3% vs. 1.8%). All other main effects and interactions favoured the null by a Bayes factor of at least 2.

Response time distribution. The delta plots for each condition in Experiment 2a are shown in Figure 9 and the results of the linear trend analyses are presented in Table 2. As in Experiment 1a, the effect size for responses made between straight hands at the shortest SOA increased linearly across the response time distribution. At the longer SOA, responses made between hands trended in the negative direction, though the support for this linear trend was only anecdotal. For responses made within one hand, the effect size remained flat across the response time distribution for both SOAs.

Table 2. Results of linear trend analyses for Experiment 2a

Response mode	SOA	Mean weighted sum	*BF*
Between hands	100 ms	10 ms	16.2 in favour of alt.
Between hands	500 ms	-8 ms	1.6 in favour of alt.
Within hand	100 ms	-1 ms	6.1 in favour of null
Within hand	500 ms	1 ms	6.2 in favour of null

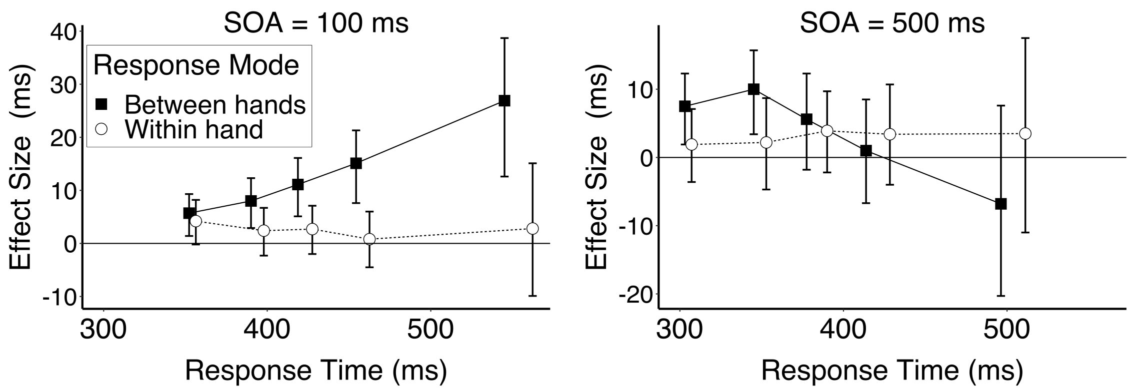

Figure 9. Response time delta plot for the spatial compatibility effect in Experiment 2a.

Experiment 2b results

Response time. An analysis of the response time data was conducted with the factors of SOA and anatomical compatibility. The mean response time as well as percent error in each condition is presented in Figure 10. The response time data did not meet sphericity assumption (ε = .58) so a BIC approximation of the Bayes factor was produced for each main effect and the interaction. Consistent with earlier experiments there was very strong evidence for a main effect of SOA (*BF* > 1,000). There was also very strong evidence in support of an anatomical compatibility effect (*BF* = 714.3). Anatomically compatible responses were faster (420 ms) than incompatible responses (428 ms). The interaction between SOA and anatomical compatibility favoured the null by a Bayes factor of 4.8.

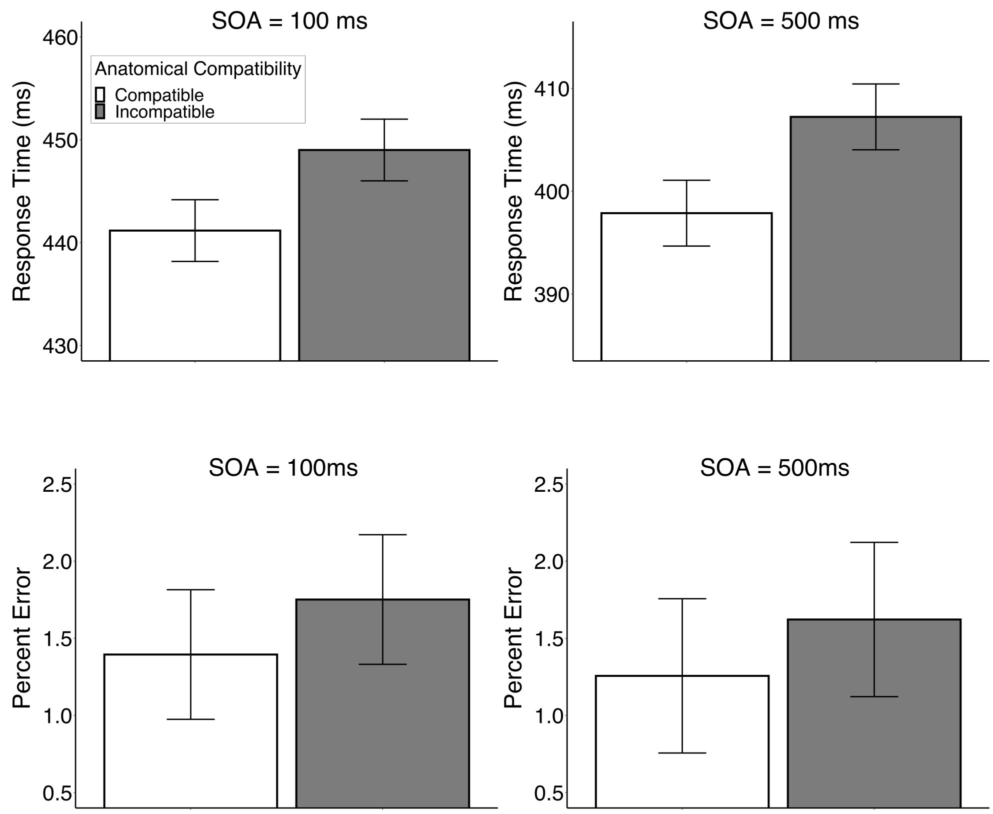

Figure 10. Mean response time and percent error in Experiment 2b as a function of SOA and compatibility between the laterality of the hand cue and the laterality of the correct response hand.

Percent error. The percent error data met the sphericity assumption (ε = .88). For both of the main effects and the interaction the null model was favoured by a factor of at least 2.

Response time distribution. The delta plots of the effect size for each SOA across the response time distribution are shown in Figure 11. Linear trend analyses for these effects are most consistent with an interpretation that the delta plots are flat for both the short SOA (mean weighted sum = 0 ms ; *BF* = 6.4 in favour of the null) and the long SOA (mean weighted sum = 4 ms; *BF* = 1.6 in favour of the null).

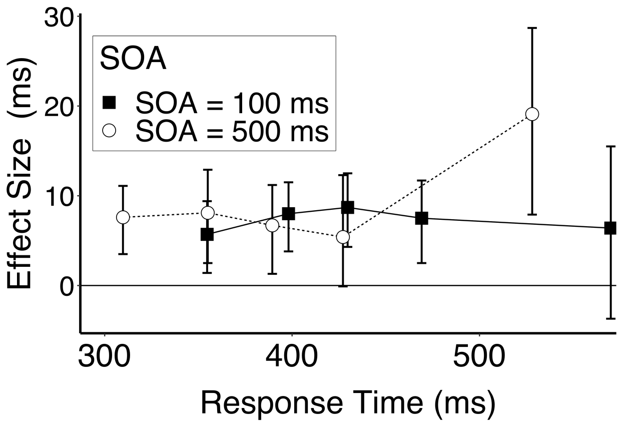

Figure 11. Response time delta plot for the anatomical compatibility effect in Experiment 2b.

Discussion

The results of Experiment 2 further support my assertion that passively viewed egocentric hand primes evoke effector-based representations. The response time and the response time distribution results from the straight-hands response mode in Experiment 1a were generally replicated with the between-hands response mode in Experiment 2a. The difference between these results was that the response time effect diminished by the long SOA in Experiment 2a. Overall however, the SRC effect obtained under these conditions appears to be small in magnitude, yet reliable at the shorter SOA.

Vainio and Mustonen (2011) obtained a null SRC effect when responses were made within a single hand, and presented this finding as positive evidence that SRC effects generated by task-irrelevant hand images are effector specific. I have introduced two criticisms of their approach. First, it is inappropriate to conclude that failing to reject the null hypothesis provides evidence in favour of the alternative. To avoid this issue in Experiment 2a, I calculated an approximation of the Bayes factor and found that the null hypothesis is more likely to account for the data than the alternative by a factor of 2.3. A Bayes factor of this size is considered to provide evidence that is merely anecdotal in nature. I therefore cannot make any strong claims about the nature of the effect obtained under a within-hand response mode condition, except to say that there is not clear evidence in favour of the presence of an effect or in favour of the absence of the effect. Second, there remains the potential that effector-specific effects might be translated into key based response code, if an effector-specific mapping option is not available. I do not have evidence that such a translation of response codes has occurred here, though the mean responses times do trend in the direction of the effect that would be expected if such a translation were to occur.

In Experiment 2b I introduced a vertical response mode, not only to assess another type of method that could be used to distinguish between spatial- and effector-based SRC accounts, but to test the hypothesis that the lateralized nature of a task requiring left-right keypress responses might be responsible for, or contribute to, the effect of the depicted hand's laterality on the response. There was a clear effect of anatomical compatibility, indicating that even in the absence of lateralized left-right spatial task component, that effector-specific SRC effects can emerge. Of course, it is not possible to completely eliminate lateralized task-demands in this methodology that requires left/right hand responses. Therefore, any claim that I am able to make about the automaticity of SRC effects or of representations evoked by a depicted hand must be interpreted as existing within a task context which includes a lateralized component. Taken together, the results of Experiment 2 show clear evidence that effector-based representations can be evoked by hand images even in the absence of any laterality judgment or other hand-image task, and in the absence of lateralized left/right response keys.

Experiment 3

Experiments 1 and 2 made use of a single hand posture (the power-grasp). I demonstrated that when hand images depicting this posture are presented in a task-irrelevant manner they can produce effector-specific SRC effects. Now that an understanding of the nature of the representation evoked by power-grasp hands has been established, I can move to investigate SRC effects evoked by other types of hand images. By testing other hand images I aim not only to increase the generalizability of my findings, but also to build an understanding of how visual features of a hand image might determine the nature of the representation evoked by that hand image. For example, how might an image of a hand be represented if it involves a pointing finger?

Like an arrow, a pointing finger acts as a spatial cue and reflexively draws attention to the side of space to which it is pointing (Ariga & Watanabe, 2009). Nishimura and Michimata (2013) used a paradigm similar to the one used in this thesis to investigate the most interesting question of what type of representations are evoked by an image of a hand that acts also as a spatial pointer. Participants in their experiment responded to the colour of a dot superimposed on a hand that had either the index or fifth finger extended pointing to the left or right side of space (see Figure 12). Participants viewed a hand image for 560 ms before coloured dot cue appeared, which remained in view until a colour-judgment response was made via a straight-hands keypress response. Under these conditions, a (surprisingly small) spatial compatibility effect of 6 ms was present, with faster responses made when the direction of point corresponded to the response key/hand. Additionally, a small (5 ms) additive effect of effector compatibility emerged. The authors interpreted their results as evidence that the hand image evokes both a spatial and an effector-specific representation. There is however, a potential problem with interpreting the apparent hand-based effect in this experiment as effector-specific, without implementing a response-mode manipulation that would allow for spatial and effector-specific SRC effects to be discriminated. This issue stems from the fact that the two views of the hand (back and palm) are visually distinct from one another on more dimensions than those used to determine spatial and anatomical compatibility. To illustrate why this is a potential confound we can conduct a thought experiment based on a seemingly reasonable, but untested, assumption that any visible finger can generate a spatial code corresponding to the direction in which that finger points. The back view of a pointing hand would generate only one spatial code, in the direction that the index finger is pointing. The palm view of the hand might however generate two spatial codes, one in the direction that the index finger is pointing, and one in the opposite direction, in which the middle, ring, and fifth finger are pointing. It would be plausible that the fastest trials would be those in which the index finger pointed to the direction corresponding with response, with the fastest response elicited by the back view of the hand, which does not also evoke a conflicting spatial code. When the direction that the index finger points does not correspond to the response, it is plausible that if the image also evokes another spatial code which is compatible with the response (the palm view), then this would facilitate responses. The pattern of results in this hypothetical experiment would look just like the pattern obtained by Nishimura and Michamata, but the apparent “effector-compatibility” effect could instead be understood as the contribution of two spatial effects. As such, the evidence presented by Nishimura and Michamata is not conclusive in establishing whether hand images can generate both spatial and effector-based SRC effects simultaneously.

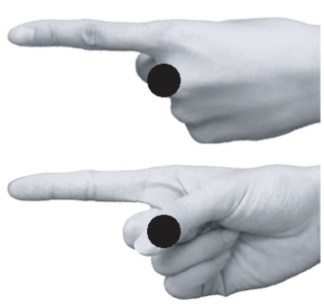

Figure 12. Sample hand stimuli from Nishimura and Michimata (2013). Note that figure images are in black and white, in the experiment the dot cue was presented to subjects in colour.

Evaluating the role of visuospatial properties of a hand stimulus is not limited to cases of hands that are explicitly pointing to the left or right. Vainio and Mustonen (2011) reported that a variety of different hand postures (see Figure 1b) produced positive SRC effects, although the time course and magnitude of these effects was modulated by hand posture. Their power-grasp posture generated SRC effects that were present at the shortest SOA and did not grow as SOA increased. In contrast, precision-grip and press-posture hands did not generate SRC effects at the shortest SOA, and the effects grew by the 400-ms SOA. Further, the largest effect generated by the power-grasp hand did not exceed 15 ms, whereas the other postures generated effects that, at their peak, were nearly twice as large. The authors provided no further discussion or investigation of these differences beyond acknowledging that they are potentially interesting. I propose that these differences in the SRC effects generated by various postures are indeed very interesting – and might reflect differences in the underlying representations evoked by the different hand postures based on the difference in their visual properties.

Vainio and Mustonen’s (2011) precision-grip and press-position hands are highly asymmetrical, as the digits on only one side of the hand are extended. This could potentially drive attention to the side of the hand on which the fingers are extended, or to the side of space into which the fingers extend. However, this hypothesis appears to conflict with Vainio and Mustonen’s data, which show stronger results for these more asymmetrical hand postures – when one would expect that if the outstretched fingers generated a spatial code these effects should be weaker overall, based on conflict between the spatial and anatomical codes. One could also hypothesize that the laterality-based and spatial-based effects have different temporal dynamics, and the slow-growing SRC effect reflects early spatial coding, and later effector-based coding of the stimulus. If spatial effects develop more strongly and rapidly than effector-based representations, and diminished more quickly, then the competition between those representations could account for the apparent lack of an SRC effect at the short SOA for press-posture and precision-grip hand images, as well as the apparent late emergence of the SRC effect for those postures, compared to the power grasp.

Given this uncertainty about the nature of the representations underlying the SRC effects reported by Vainio and Mustonen (2011), the primary aim of Experiment 3 was to explore the time course, direction, and effector-specificity of SRC effects elicited by press-posture images. In Experiment 3a both the palm and back view of this hand posture were presented, to allow for comparisons to be made between cases in which the spatial location of the fingers competes with laterality (back view), to when they do not compete (palm view). These two hand views were randomly intermixed. The results of this experiment included an unexpected reversal of the compatibility effect reported by Vainio and Mustonen (2011), generated by similar back view press posture stimuli. Additionally, the effects were in the direction opposite to those obtained in response to power-grasp images in Experiments 1 and 2. I considered the possibility that this result may have arisen due to the intermixing of palm and back view stimuli, as Vainio and Mustonen did not mix stimulus views within an experiment. Therefore, in Experiment 3b the view of the hand was blocked. Separating back and palm views did not influence the direction of the effects. In Experiment 3c, only back-view stimuli were presented, and a vertical response mode was utilized in an effort to determine whether eliminating the possibility of spatially coding the response options would allow an effector-specific effect to emerge. This method was also unsuccessful in reversing the direction of the effect.

Method

Participants. In each of Experiments 3a and 3b, 48 students who had not participated in another version of this experiment were recruited from the same participant pool used in Experiments 1 and 2. In Experiment 3c, 60 participants were recruited from Prolific.co, a website where individuals interested in research participation sign up to participate in research studies and receive monetary compensation. This change to the participant recruitment pool and procedure was made in response to the need to conduct online experiments during the COVID-19 pandemic. I also increased the target sample size from 48 participants to 60 for experiments conducted online, in anticipation of a higher rate of variability in the data, as well as a potentially greater need to reject data from participants completing experiments without experimenter supervision.

Given that participants completing online experiments were not observed, upon completing an online task, participants were asked to report whether they followed the instructions for the entire duration of the experiment (it was made explicit that their response would not have an impact on their compensation and was for reporting purposes only, to encourage honest reporting). Data from any participant indicating that they did not always follow the experimental instructions were removed prior to any further analysis. Additionally, participants in Experiment 3c were asked to report whether the *7* and *N* keys on their keyboard (which were used as response keys in the vertical response mode) were approximately vertically aligned, and data from any participant indicating the keys were horizontally displaced by more than 1 full key width were excluded from analysis. Additionally, for online studies (3c) the mean critical correct RT was computed for each participant, and any participants with a mean RT greater than 1,000 ms were removed from the study prior to further analysis. The standard exclusion threshold of 80% task accuracy was applied to all versions of Experiment 3.

After applying the exclusion criteria, data from all 48 participants were included in the analysis for both Experiments 3a and 3b. Experiment 3c had a final sample of 49 participants (5 participants were removed for failing to follow instructions, 4 were removed due to horizontal displacement of their response keys, 1 participant was excluded for failing to obtain at least 80% accuracy on the task, and 1 participant had a mean correct RT greater than 1,000 ms). Of the remaining 145 participants across all 3 versions of the experiment, 82 were female, 128 were right handed, and the median age of the participants was 32 yr (range from 18- 56 yr).

Materials. Greyscale photographs of a hand with the index finger and thumb extended (a press posture) were taken from an overhead position. A view of the back of the hand was used in all three versions of the experiment, depicting the outstretched thumb and index finger, and the proximal phalanges of the remaining 3 fingers. A palm view of this hand posture was also shown in Experiments 3a and 3b, which showed the palmar surface of the hand, thumb, and index finger, as well as the dorsal surface of the distal and middle phalanges of the three remaining fingers (see Figure 13). The other-laterality version of these stimuli were generated by horizontally mirroring the original images. The dimensions of these hands were approximately 150 x 256 pixels. Versions that included the colour dot were created by placing a coloured dot of approximately 50 pixels in diameter near the center of the non-finger portion of the hand. This placement allowed for an unobstructed view of all fingers for both the back and palm stimulus views.

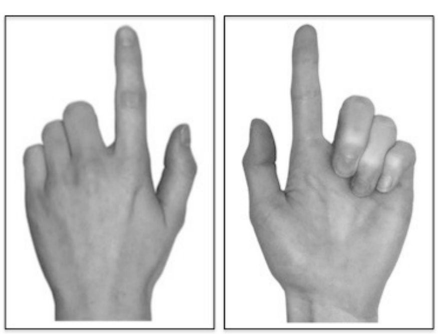

Figure 13. Sample press-posture stimuli. Left hands in back-view and palm-view.

Procedure. The procedure for Experiments 3a and 3b was identical to Experiment 1a, except that responses were made only in a straight-hands response mode. Participants saw two versions of the press-posture stimuli (back view and palm view). Therefore, the number of critical trials remained the same as in Experiment 1a (320), as did the number of repetitions of each unique trial, as the number of unique trials doubled with the introduction of the stimulus view manipulation. In Experiment 3a both stimulus views were shown randomly intermixed within a single critical block. In Experiment 3b stimulus view was held constant within a block and varied between the two experimental blocks. Block order was counterbalanced between participants.

The procedure in Experiment 3c was modified from Experiment 2b to suit an online testing environment. Participants completed the experiment on either a desktop or laptop computer. Participants were instructed to put the browser window that contained the experiment into full-screen mode before beginning the task. Participants were instructed to respond using the *7* key on the top of the keyboard and the *N* key. These keys were selected due to their approximate vertical alignment on a standard keyboard. Assignment of response hands to keys was varied between participants, but was held constant within the experiment for each participant. Participants completed a single block of trials, in which each of the 8 unique stimulus configurations (left/right hand, back/palm view, blue/green [or orange/purple] colour) was repeated in random order 32 times, for a total of 256 critical trials. Self-paced rest breaks occurred every 32 trials, rather than the standard 40 trials.

Results

Averaging across all three versions of Experiment 3, mean accuracy on the colour dot task was 97%, and ranged from 89-100% correct. Following the outlier removal procedure described in Experiment 1, response times less than 100 ms were removed from all experiments, whereas the upper bound was set at 1,200 ms, 1,100 ms, and 1,300 ms for Experiments 3a, 3b, and 3c, respectively. Incorrect trials were also removed from the response time analysis.

Experiment 3a results

Response time. An analysis of RT data included the factors of SOA, stimulus view, and anatomical compatibility. The mean response time as well as percent error in each condition is presented in Figure 14. The response time data did not meet the sphericity assumption ($\varepsilon = 0.29$), so I used a BIC approximation of the Bayes factor. The analysis provided very strong evidence for a main effect of SOA in the same direction as seen in all earlier experiments ($BF > 1{,}000$). There was also anecdotal evidence of a main effect of anatomical compatibility ($BF = 1.8$ in favour of the alternative). Notably, the direction of this effect shows faster responses were made under incompatible conditions (429 ms) than compatible (432 ms). The direction of this effect is therefore in the opposite direction relative to the effects generated by egocentrically presented power-grasp hands.

There was no evidence in favour of a main effect of hand view ($BF = 2.4$ in favour of the null). Critically, evidence for an interaction between hand view and hand compatibility was very strong ($BF = 233.5$). The response time means indicted a crossover interaction. Separate analyses for each view indicated that the back view of the hand generated a negative compatibility effect. Responses were made more quickly when the laterality of the depicted hand and the response hand did not match (427 ms) compared to when they did match (437 ms; *BF* = 217.4). The palm view generated a positive compatibility effect, in which a match between the depicted and response hand led to faster responses on average (427 ms) compared to when they did not match (432 ms).

Additionally, the full model analysis indicated strong evidence for the 3-way interaction between view, anatomical compatibility, and SOA (*BF* = 29.4). For the back view of the hand the compatibility effect was not significantly modulated by SOA (*BF* = 1.5 in favour of the null), though the pattern of the means shows a larger effect size at the longer SOA (-14 ms) than at the shorter SOA (-6). For the palm view of the hand there is positive evidence of an interaction between SOA and anatomical compatibility (*BF* = 3.4). The compatibility effect appears to be absent at the shorter SOA (0 ms) and present at the longer SOA (8 ms).

Though the data in this experiment were coded in terms of the anatomical laterality of the depicted hand, it is important to note that these results can also be interpreted in regard to the spatial location of the outstretched fingers on the hand. Given that the laterality of the hand matches the location of the salient fingers in the palm view, but not in the back view, a more parsimonious interpretation of these results is that both views of the hand generated a positive compatibility effect between the location of the outstretched fingers and response location (or response hand, we cannot distinguish between these two possibilities in a straight-hands response mode design).

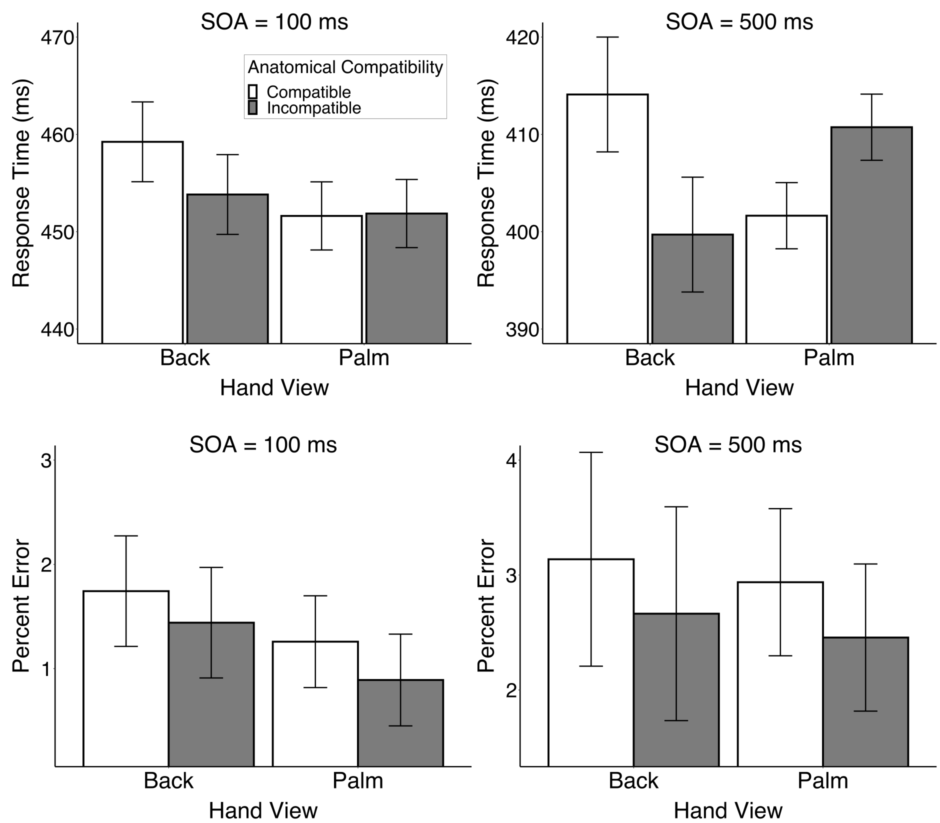

Figure 14. Mean response time and percent error in Experiment 3a as a function of SOA and compatibility between the laterality of the hand cue and the laterality of the correct response hand.

Percent error. The percent error data did not meet the sphericity assumption (ε = 0.65). The BIC approximation revealed that the null model was favoured for all main effects and interactions, with the exception of SOA. More errors were made at the long SOA (2.8%) than at the short SOA (1.3%; *BF* > 1,000).

Response Time Distribution. The delta plots for each SOA by hand view condition are shown in Figure 15, and the results of the linear trend analyses for these delta plots are listed in table 3. There is weak evidence in favour of a negative linear trend for the back view of the hand at the longer SOA only. The evidence for all other conditions favours an interpretation of the delta plots as being flat.

Table 3. Results of linear trend analyses for Experiment 3a.

Hand view	SOA	Mean weighted sum	*BF*
Back	100 ms	-2 ms	6.4 in favour of null
Palm	100 ms	0 ms	6.3 in favour of null
Back	500 ms	-11 ms	3.0 in favour of alt
Palm	500 ms	7 ms	1.2 in favour of null

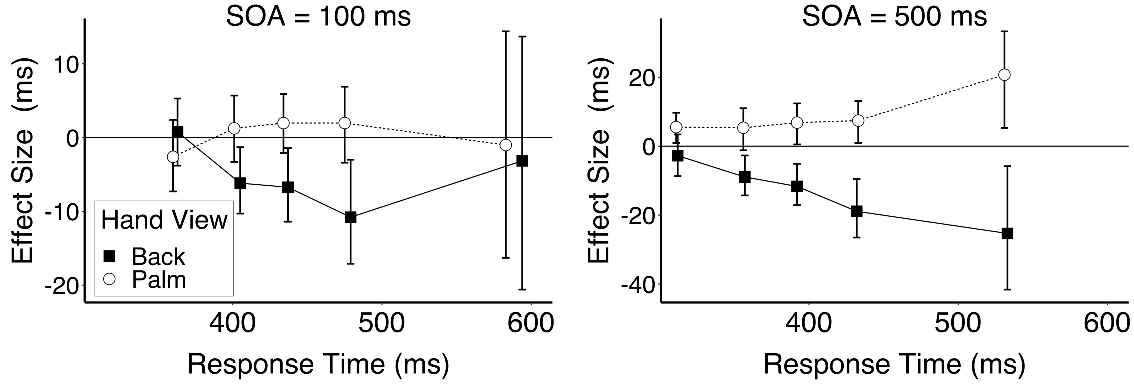

Figure 15. Response time delta plot for the anatomical compatibility effect in Experiment 3a.

Experiment 3b results

Response time. An analysis of RT data included the factors of SOA, stimulus view, and anatomical compatibility. These data did not meet the sphericity assumption ($\varepsilon = 0.53$). The BIC approximation procedure revealed very strong evidence in favour of a main effect of SOA (*BF* > 1,000). The interaction of interest between view and anatomical compatibility favoured the alternative, but only anecdotally (*BF* = 2.0). All other main effects and interactions favoured the null by a factor of at least 2.

Separate analysis for each view of the hand revealed that in the back-view block the anatomical compatibility effect was not present (*BF* = 3.0). The pattern of mean RTs revealed a similar pattern to that seen in Experiment 3a, in which incompatible responses were made faster (438 ms) than compatible responses (443 ms). There was positive evidence of a main effect of anatomically compatibility in the palm-view block of trials (*BF* = 7.1). In this case, compatible responses were on average made more quickly (435 ms) than incompatible responses (422 ms).

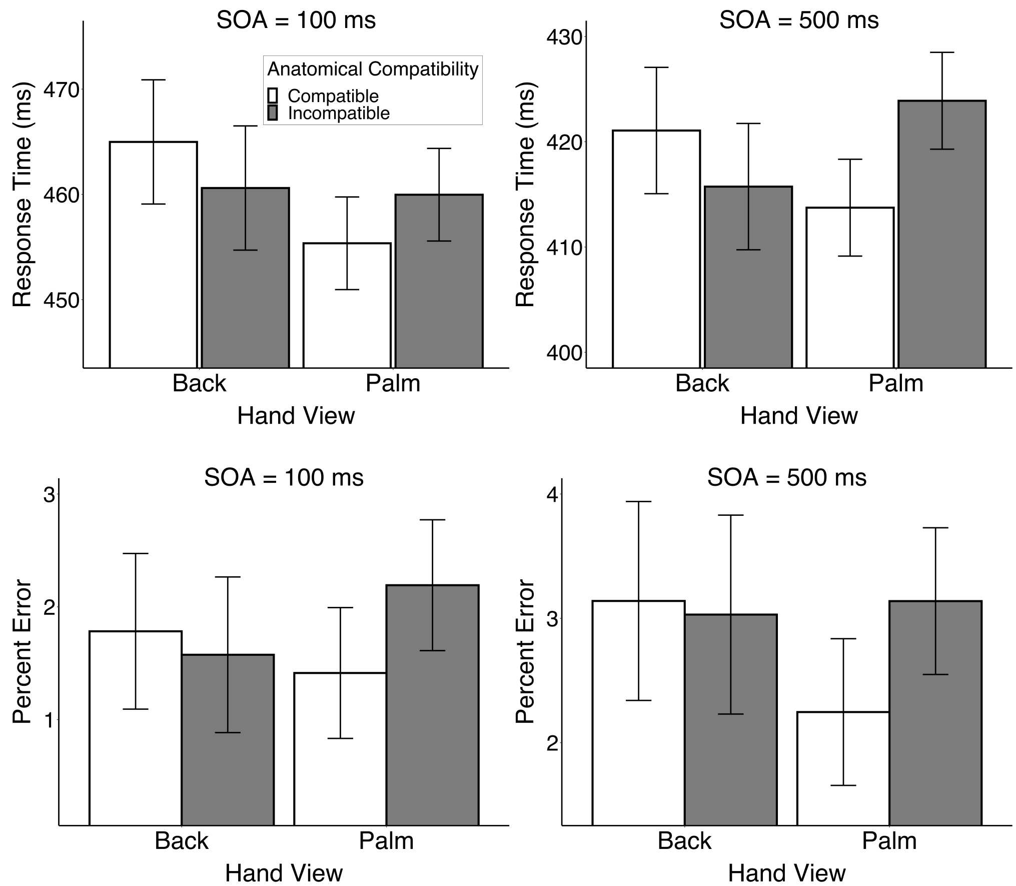

Figure 16. Mean response time and percent error in Experiment 3b as a function of SOA and compatibility between the laterality of the hand cue and the laterality of the correct response hand.

Percent error. The percent error data met the sphericity assumption ($\varepsilon = 0.75$). A main effect of SOA was strongly supported (*BF* > 1,000). There was no evidence in support of a main effect of anatomical compatibility (*BF* = 3.4) or view (*BF* = 7.0), nor for the view by compatibility interaction (*BF*= 1.1 for alt). Both of the other interactions favoured the null by a Bayes factor of at least 3.

Response time distribution. The delta plots for each SOA by hand view condition are shown in Figure 17, and the results of the linear trend analyses for these delta plots are listed in Table 4. For all conditions, the evidence favours an interpretation of flat effects across the response time distribution.

Table 4. Results of linear trend analyses for Experiment 3b.

Hand view	SOA	Mean weighted sum	*BF*
Back	100 ms	3 ms	5.5 in favour of null
Back	500 ms	-2 ms	5.6 in favour of null
Palm	100 ms	-4 ms	4.0 in favour of null
Palm	500 ms	0 ms	6.3 in favour of null

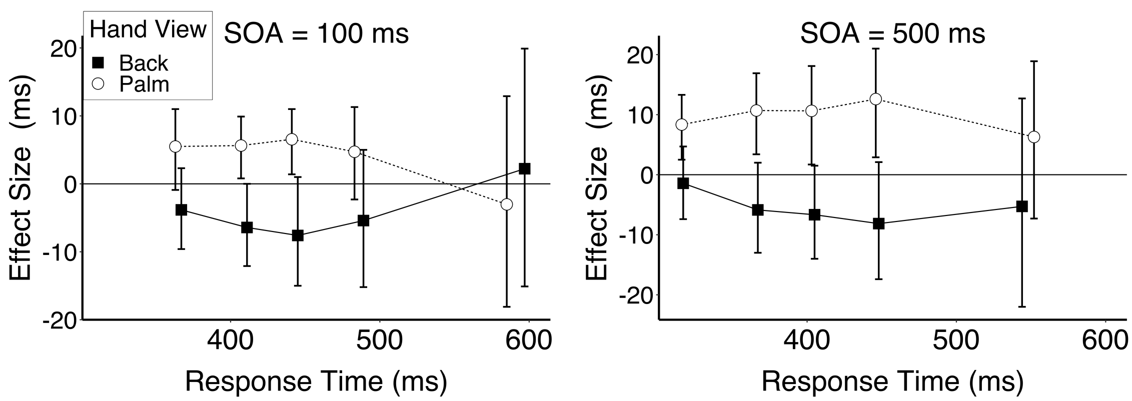

Figure 17. Response time delta plot for the anatomical compatibility effect in Experiment 3b.

Experiment 3c results

Response time. An analysis of RT data included the factors of SOA and anatomical compatibility. The response time data did not meet the sphericity assumption ($\varepsilon = 0.66$) therefore the BIC was used to approximate the main effects of SOA and anatomical compatibility, as well as their interaction. There was very strong evidence for a main effect of SOA (*BF* > 1,000*).* There was no evidence in support of a main effect of anatomical compatibility (*BF* = 2.1 in favour of the null) or an interaction between compatibility and SOA (*BF* = 4.6 in favour of the null). Separate analyses for each SOA also produced evidence in favour of a null effect of compatibility (*BF* = 1.5 and 6.3, for 100 ms and 500 ms SOA, respectively).

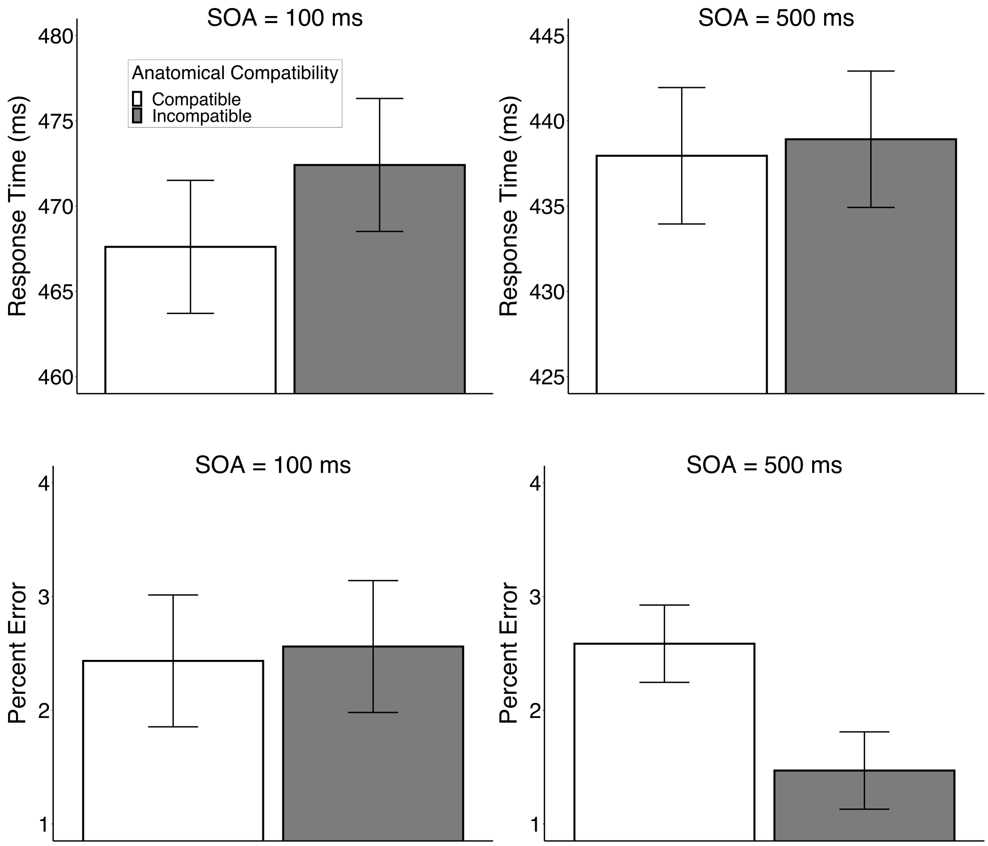

Figure 18. Mean response time and percent error in Experiment 3c as a function of SOA and compatibility between the laterality of the hand cue and the laterality of the correct response hand.

Percent error. The percent error data met the sphericity assumption ($\varepsilon = 0.96$). The analysis produced no evidence for a main effect of SOA (*BF* = 2.1 in favour of the null), or anatomical compatibility (*BF* = 1.9 in favour of the null). The alternative hypothesis was favoured over the null in regards to the presence of an interaction between SOA and compatibility – but only anecdotally (*BF* = 1.3**)**. Separate analyses for each SOA reveled evidence of a null compatibility effect at the short SOA (*BF* = 4.5). At the long SOA there is positive evidence in favour of an effect of compatibility (*BF* = 7.6), with fewer errors made in the incompatible (1.4%) than compatible (2.6%) condition.

Response time distribution. The effect size by quintile at each SOA is shown in Figure 19. The linear trend analyses favoured a flat interpretation of the delta plots for both the short SOA (mean weighted sum = 6 ms, *BF* = 1.6 in favour of the null) and the longer SOA (mean weighted sum = 0 ms, *BF* = 6.4 in favour of the null).

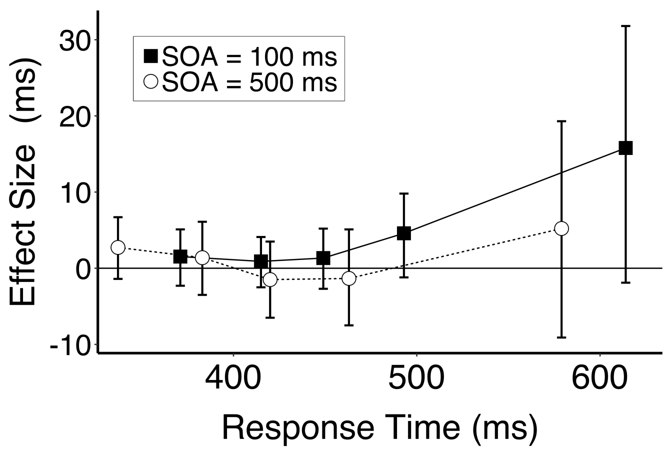

Figure 19. Response time delta plot for the compatibility effect in Experiment 3c.

Discussion

Changing the posture of the task-irrelevant hand image from a closed power grasp to a press posture in Experiment 3 produced a most unexpected and interesting set of results. The SRC effect generated by palm view press-posture hands appears at first to be consistent with the expectation that a hand-image prime will facilitate a response made with the same-laterality hand, as seen in the earlier experiments as well as those presented by Vainio and Mustonen (2011). However, upon inspection of the SRC effect generated by the back view of these hands, another interpretation of these results becomes more likely. That is, the SRC effects produced by the press posture hands appear to be more consistent with the interpretation that compatibility emerges on the basis of correspondence between the location of the response key, and the spatial location of the outstretched forefinger and thumb of the depicted hand. This interpretation is more parsimonious than the interpretation that these effects are driven by the laterality of the depicted hand, as it allows us to interpret the SRC effect generated by both views of the hand as being positive, rather than reversing for the back-view stimuli.

In an effort to test for effector-based coding of the responses, Experiment 3c utilized a vertical response mode, so that the response keys could not be coded according to the left/right location of the key. Even under these conditions, a laterality-based SRC effect did not emerge. This is especially notable as the hand postures depicted on the screen closely matched the likely posture of the participants' own hands while they made their responses. This evidence suggests that effector-specific representations are not automatically or obligatorily evoked by all task-irrelevant hand images, even when one is in a task context of making left/right hand lateralized keypress responses. The difference between the results of Experiment 3 and Experiments 1 and 2 shows that not all hand images are equal in generating laterality-based SRC effects, and that changing the visuospatial properties of the stimuli (such as their visual asymmetry) appears to change the way in which these hand images are represented.

Experiment 4

Introduction

Parsons (1994) demonstrated that hand images depicting all manner of hand postures and orientations were represented in a motoric fashion when subjects made explicit laterality judgments of the hand images. In earlier experiments, I have demonstrated that effector-specific SRC effects can be evoked by hand images in the absence of a laterality judgment task, but only for select hand images. Hand images depicting a press hand posture in which the index finger and thumb are outstretched resist being coded in an intrinsic frame of reference – likely due to the salient spatial asymmetry of the hand image. We can therefore use these press-posture hands to further explore the nature of representations evoked under different task conditions.

In Experiment 4 participants viewed images of a hand and completed a colour-dot judgment task on 80% of experimental trials. On the remaining 20% of trials, the dot cue was uncoloured (greyscale) – which acted as a cue for participants to make a keypress response judging the laterality of the hand. This experimental design allowed me to address whether hand images that did not generate laterality-based SRC effects in Experiment 3 (press posture) will do so in this new task context, even on colour dot trials where the hand remains task-irrelevant. The nature of the representation underlying the SRC effect evoked by these images was further probed using 3 different response modes: straight hands (Experiment 4a), crossed hands (Experiment 4b), and vertical response hands (Experiment 4c). I also measured SRC effects in this same paradigm using hand images that were pointing to the left or right side of space (Experiment 4d), to examine whether the introduction of the laterality judgment task on a minority of trials encouraged effector-based coding of all hand images, even those with a very salient left/right spatial dimension.

Method

Participants. In Experiment 4a, 30 participants were recruited from the Prolific.co participant pool. This reduced sample size was selected as part of the early stage of the process of adapting to an online testing environment. After the conclusion of this experiment I chose to increase the sample size moving forward for online experiments (including the later run, but earlier presented Experiment 3c). For Experiments 4b, 4c, and 4d, 60 participants each were recruited from Prolific. Data from 28 participants were included from Experiment 4a (2 participants were excluded for a mean correct RT > 1,000 ms). In total, the data from 11 participants were excluded from Experiment 4b (1 for not meeting the accuracy threshold, 1 for reporting that they did not follow instructions, and 9 for having a mean correct RT > 1,000 ms), leading to a final sample size of 49. Experiment 4c also had a final sample size of 49 (11 participants were excluded, 1 for not meeting the accuracy threshold, 5 for reporting that they did not always follow task instructions, 2 who reported that the *N* and *7* keys they used as response keys were not approximately vertically aligned, and a further 3 participants were dropped for having mean correct RTs above 1,000 ms). Fourteen participants were excluded from Experiment 4d (1 for not meeting the 80% task accuracy threshold, 3 for reporting that they did not follow task instructions, 8 for having a mean correct RT greater than 1,000 ms, and 2 participants who had 0 correct trials for at least 1 trial type), for a total sample size of 46. Of the 172 participants retained in Experiment 4, 50 were female, 154 were right-handed, and the median age was 23 yr (range 18 to 76 yr).

Materials. Experiments 4a, 4b, and 4c used only back view, press-posture hand images, identical to those used in Experiment 3. Grey-dot versions of these stimuli were also generated and were identical to the colour-dot versions, except that the dot was greyscale and had a thin black outline (to increase contrast with the greyscale hand image). Experiment 4d used greyscale hand images depicting a closed grasp with an extended index finger pointing to either the left or right side of space. Separate images were created for the palm view of the hand (which depicted the palmar surface of the hand and outstretched index finger, as well as the dorsal surface of the distal and middle phalanges of the three remaining fingers and thumb, which were curled inwards) and the back view of the hand (in which only the dorsal surface of the hand, index finger, and the proximal phalanges of the 3 remaining fingers were in view). Opposite-hand versions of these images were created by horizontally mirroring the original images (see Figure 12). The dimensions of these hands were approximately 420 x 200 pixels. Versions that included a dot were created by placing a coloured dot of approximately 50 pixels in diameter near the center of the non-finger portion of the hand. In the palm-view version, the dot partially obstructed the view of part of the middle finger and thumb. In addition to the coloured-dot version of these images, a grey-dot version was also created. The grey-dot versions included on the hand a superimposed dot of the same size and in the same position as the coloured dots.

Procedure. In all four versions of Experiment 4, participants completed the colour-dot task on only 80% of trials. On the remaining 20% of trials, a grey dot appeared on the hand in place of a coloured dot. The ratio of grey- to colour-dot trials was maintained for all unique trial types. Coloured-dot and grey-dot trials were randomly intermixed. Participants were instructed that the grey dot was a cue to respond to the laterality of the pictured hand. Laterality-judgment responses were always made with the response hand that corresponded to the depicted hand. That is, when a grey dot appeared on a left-hand image, participants made a left-handed keypress response, and when a grey dot appeared on a right hand, participants made a right-handed keypress. In Experiment 4a, participants responded to the back view of press-posture hands using the *Z* and *M* keys, in a straight-hands response mode (left index finger on *Z*, right index finger on *M*) for the duration of the study. In Experiment 4b, participants responded using a crossed-hands response mode (left index finger on *M*, right index finger on *Z*). In Experiment 4c, participants responded in the vertical response mode with the *7* and *N* keys, and hand to key assignment was counterbalanced between participants. In Experiment 4d participants responded using the Z and M keys with straight hands (left index finger on *Z*, right index finger on *M*). Palm and back view of the horizontal pointing-hand stimuli were randomly intermixed. In all versions of Experiment 4 participants completed 320 critical trials. All other elements of the task were consistent with earlier experiments.

Results

Averaging across all four versions of Experiment 4, mean accuracy on the colour-dot task was 96%, and ranged from 82-100% correct. Mean accuracy on the laterality-judgment task was 85%, with 90%, 93%, and 87% accuracy on Experiments 4a, 4b, 4c, respective which used press postures hands, and 73% laterality judgment accuracy in Experiment 4d which you horizontal pointing hands. Following the outlier removal procedure described in Experiment 1, response times less than 100 ms were removed from all experiments, whereas the upper bound was set at 2,800 ms, 2,600 ms, 2,500 ms, and 2,700 ms for Experiments 4a, 4b, 4c, and 4d, respectively. The longer RTs in this experiment relative to earlier experiments were primarily driven by the laterality judgment trials. Incorrect trials were removed from the response time analysis.

Experiment 4a results

Overall response time. An analysis of the response time data was conducted including SOA and cue type (colour or laterality judgment) as factors. These data did not meet the sphericity assumption (ε = 0.37), so the BIC approximation procedure was applied. There was very strong evidence of a main effect of SOA (*BF* > 1,000) and cue type (*BF* > 1,000), in which colour-judgment responses were made more quickly (562 ms) than laterality judgments (944 ms). An interaction between SOA and cue type was supported by the analysis (*BF* = 5.2), and the response time advantage for the colour-dot trials was longer at the short SOA (366 ms difference) than the long SOA (397 ms difference). These results suggest that participants were not making explicit laterality judgments on each trial prior to the onset of the colour cue, but that the process of explicitly judging the hand occurred after the onset of the grey-dot cue.

Colour-dot response time. An analysis of the colour-dot response time data was conducted including SOA and anatomical compatibility as factors. These data met the sphericity assumption (ε = 0.81). A main effect of SOA was strongly supported (*BF* > 1,000). Additionally, the main effect of anatomical compatibility was strongly supported (*BF* > 1,000). When the laterality of the depicted and response hands matched, responses were made more quickly (546 ms) compared to when they did not match (579 ms). Notably, this effect is larger in magnitude and in the opposite direction of the effect generated by the back view of press hands in Experiments 3a and 3b under task demands that did not require attention to be paid to the laterality of the stimulus hand. The evidence of an interaction between compatibility and SOA anecdotally favoured the null (*BF* = 2.2).

Percent error. The percent error data did not meet the sphericity assumption (ε = 0.65). The BIC approximation of the Bayes factor produced positive evidence of a main effect of anatomical compatibility, in which fewer errors were made under compatible (2.6%) compared to incompatible (6.0%) conditions. There was no evidence of a main effect of SOA on error rates (*BF* = 2.1 in favour of the null) and evidence for an interaction between the two factors anecdotally favoured the alternative (*BF* = 1.1).

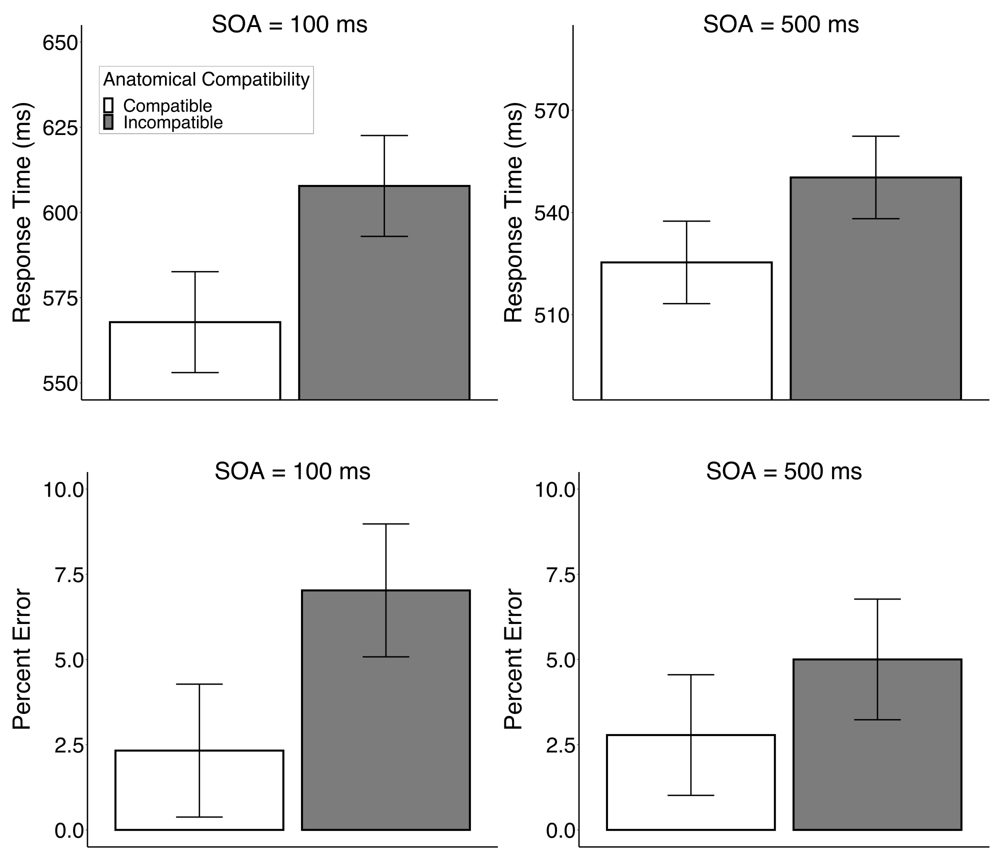

Figure 20. Mean response time and percent error in Experiment 4a as a function of SOA and compatibility between the laterality of the hand cue and the laterality of the correct response hand on colour dot trials.

Response time distribution. The compatibility effect size for colour-dot trials by quintile for each SOA is shown in Figure 19. At the shorter SOA, the effect linearly increased across the reaction time distribution (mean weighted sum = 27 ms; *BF* = 3.2). At the longer SOA, the effect was not significantly different from a flat pattern across quintiles (mean weighted sum = 10 ms; *BF* = 3.1 in favour of the null).

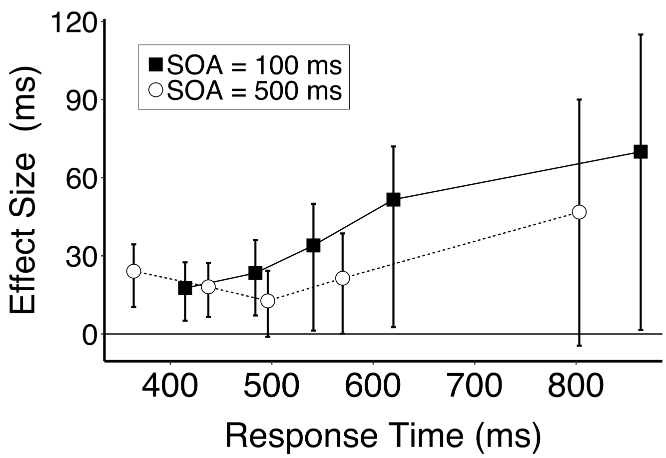

Figure 21. Response time delta plot for the compatibility effect in Experiment 4a.

Experiment 4b results

Overall response time. An analysis of the response time data was conducted including SOA and cue as factors. These data did not meet the sphericity assumption (ε = 0.40), so the BIC approximation procedure was applied. There was very strong evidence of a main effect of SOA (*BF* > 1,000) and cue type (*BF* > 1,000), in which colour-judgment responses were made more quickly (594 ms) than laterality judgments (924 ms). An interaction between SOA and cue type was not supported by the analysis (*BF* = 2.8 in favour of the null).

Colour-dot response time. An analysis of the colour dot response time was conducted including SOA and anatomical compatibility as factors. Mean response times and error rates for each condition are shown in Figure 22. These data met the sphericity assumption ($\varepsilon = 0.89$). A main effect of SOA was strongly supported with a Bayes factor greater than 1,000. A main effect of anatomical compatibility was also strongly supported ($BF > 1{,}000$). Anatomically compatible responses were made more quickly (576 ms) than incompatible responses (614 ms). Anatomical compatibility and SOA did not interact ($BF = 4.6$).

Percent error. The percent error data did not meet the sphericity assumption ($\varepsilon = 0.69$). The BIC approximation procedure generated very strong evidence for a main effect of anatomical compatibility ($BF > 1{,}000$). More errors were made under incompatible compared to compatible conditions. Errors were not modulated by SOA ($BF = 2.7$ in favour of the null). There was anecdotal support for the interaction between compatibility and SOA ($BF = 2.9$), though at both SOAs the pattern of error results was the same, the difference in error rates was more exaggerated at the shorter SOA.

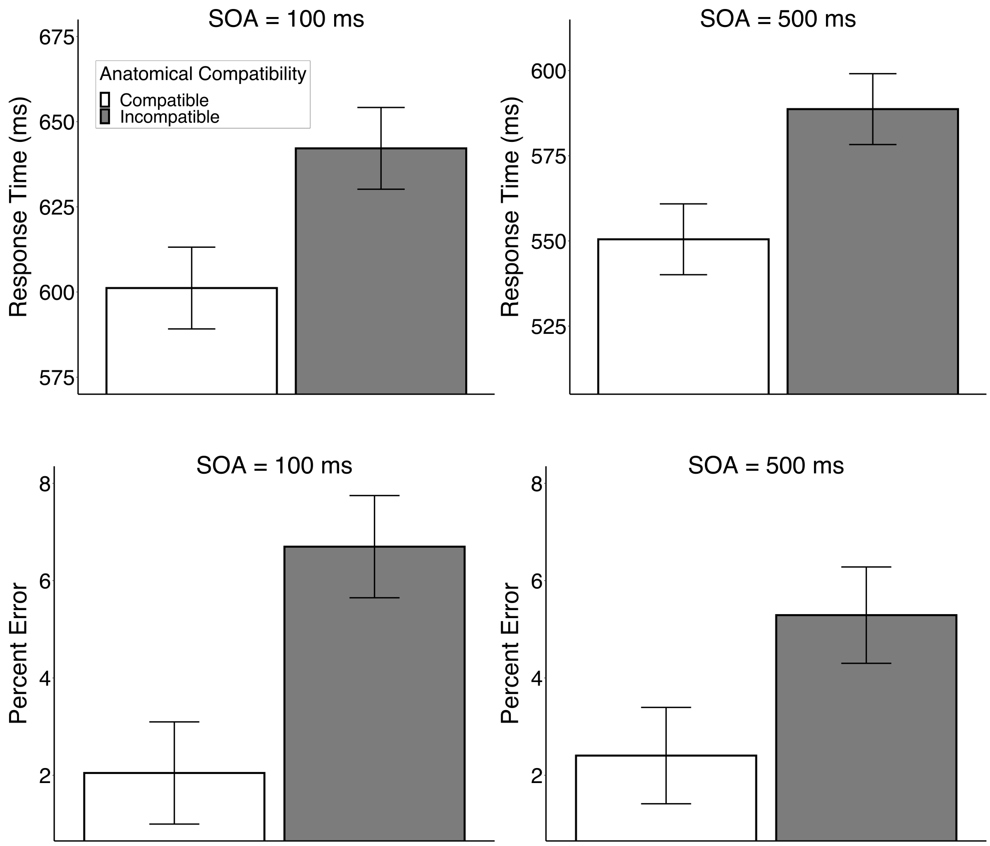

Figure 22. Mean response time and percent error in Experiment 4b as a function of SOA and compatibility between the laterality of the hand cue and the laterality of the correct response hand on colour dot trials.

Response time distribution. The compatibility effect size across quintiles for each SOA is shown in Figure 23. There was no support for a linear trend in the delta plot for either the shorter or longer SOA (mean weighted sum = 10 ms for both SOAs; *BF* = 3.6 and 3.7, respectively, in favour of the null).

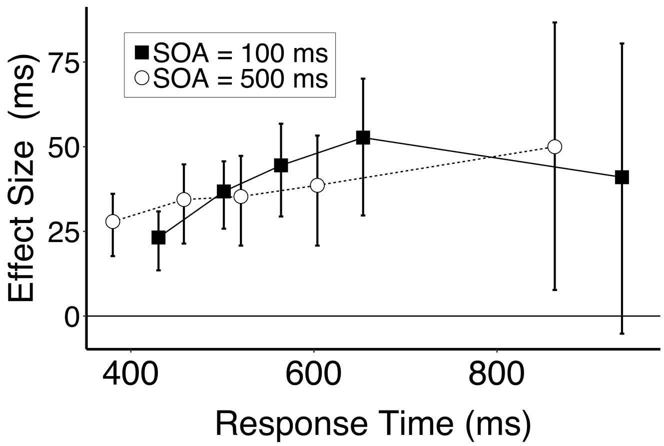

Figure 23. Response time delta plot for the compatibility effect in Experiment 4b.

Experiment 4c results

Overall response time. An analysis of the response time data was conducted including SOA and cue as factors. These data did not meet the sphericity assumption (ε = 0.54), so the BIC approximation procedure was applied. There was very strong evidence of a main effect of cue type (*BF* > 1,000), in which colour-judgment responses were made more quickly (613 ms) than laterality judgments (1000 ms). Evidence for a main effect of SOA anecdotally favoured the null (*BF* = 1.5), as the interaction between SOA and cue type favoured the null as well (*BF* = 4.1).

Colour-dot response time. An analysis of the colour-judgment RT data included the factors of SOA and anatomical compatibility. The response time data met the sphericity assumption (ε = 0.86). Critically, I obtained very strong evidence of an effect of anatomical compatibility, in which responses were made more quickly under compatible (560 ms) compared to incompatible (591 ms) conditions (*BF* > 1,000). These results closely mirror the results of Experiment 4a and 4b in which participants responded with straight- and crossed-hand response modes, rather than a vertical response mode.

There was strong evidence for a main effect of SOA (*BF* > 1,000), but the interaction between SOA and compatibility was not supported (*BF* = 4.8).

Percent error. The percent error data was analyzed in the same fashion as the colour-dot response time data. These data violated the sphericity assumption (ε = 0.61), so I used a BIC approximation of the Bayes factor. There was strong evidence of a main effect of anatomical compatibility (*BF* = 158.7). Consistent with the pattern seen in the RT data, more errors were made under anatomically incompatible conditions (5.0%) than compatible (1.9%). There was no evidence to support either a main effect of SOA (*BF* = 2.6) or an interaction between SOA and compatibility (*BF* = 4.0).

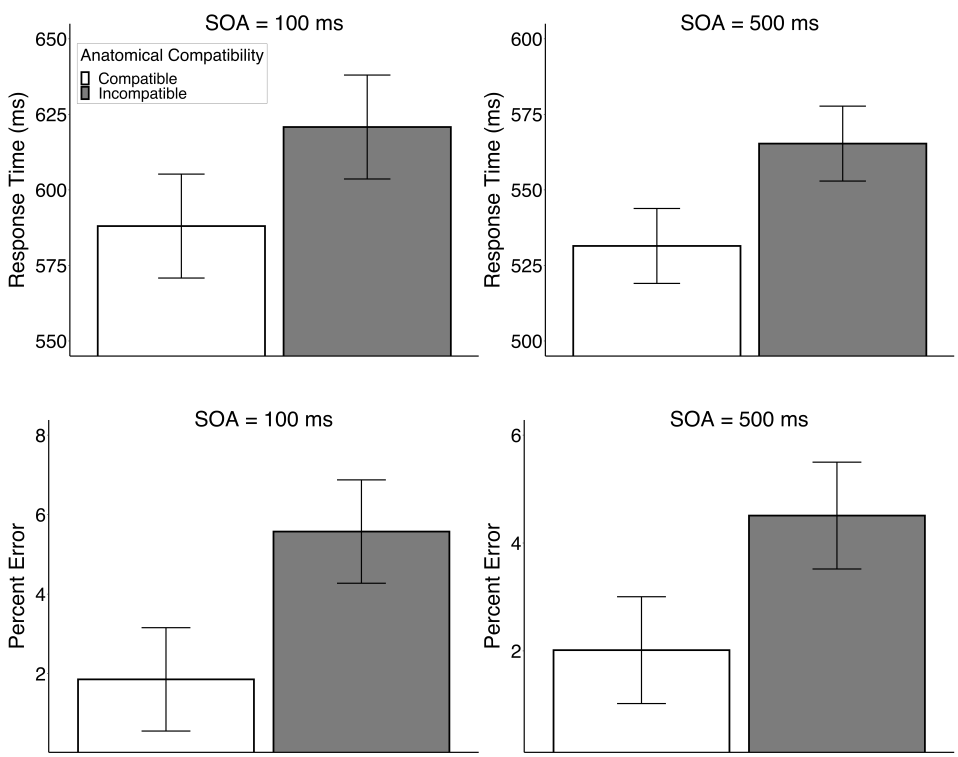

Figure 24. Mean response time and percent error in Experiment 4c as a function of SOA and compatibility between the laterality of the hand cue and the laterality of the correct response hand on colour dot trials.

Response time distribution. Consistent with the results under the straight-hands response mode in Experiment 4a, the compatibility effect size for vertical responses made at the shorter SOA grew linearly across quintiles (mean weighted sum = 56 ms ; *BF* = 15.3). At the longer SOA the effect did not significantly different from a flat trend (mean weighted sum = 19 ms ; *BF* = 3.1). Effect size across quintiles for each SOA is shown in Figure 25.

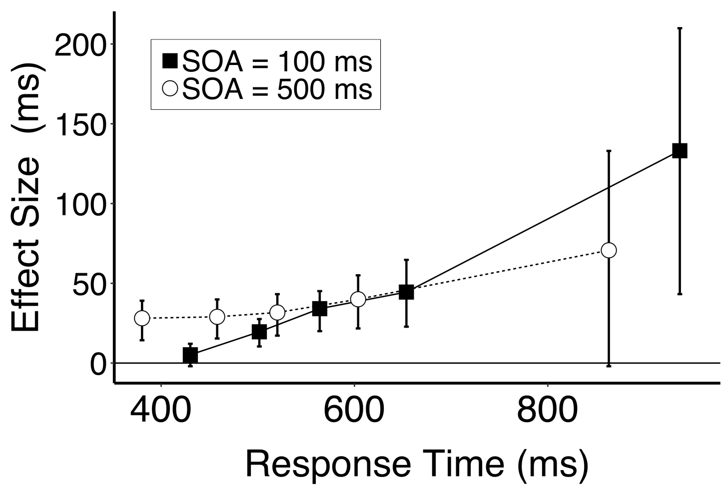

Figure 25. Response time delta plot for the compatibility effect in Experiment 4c.

Experiment 4d results

Overall response time. An analysis of the response time data was conducted including SOA, cue type, and hand view (palm or back) as factors. These data did not meet the sphericity assumption (ε = 0.25), so the BIC approximation procedure was applied. There was very strong evidence of a main effect of SOA (*BF* > 1, 000) and cue type (*BF* > 1,000), in which colour-judgment responses were made more quickly (517 ms) than laterality judgments (1044 ms). Evidence of a main effect of hand view anecdotally favoured the null (*BF* = 2.6) Evidence for all interactions favoured the null by a Bayes factor of at least 3, except for the cue type by view interaction, which only anecdotally supported the null (*BF* = 1.2). The mean RTs show a cross-over pattern, in which response time were shorter for the back-view of the hand in the colour dot condition (6 ms difference), and for the laterality judgement condition response times were shorted for the palm-view stimuli (35 ms difference).

Colour-dot response time. An analysis of the colour-judgment RT data included the factors of SOA, anatomical compatibility, and spatial alignment. Mean RTs for each condition can be seen in Figure 26. Spatial alignment was defined as a match between the location of the response key (or the laterality of the response hand, given that responses were made with straight hands) and the direction in which the depicted hand was pointing. Compatibility and alignment in this design were orthogonal, due to the inclusion of two views of each hand (for example, a left hand may point to the left or right side of space depending on whether the view shows the back or the palm of the hand), though it is important to note that not all conditions have the same visual components. That is, when compatibility and alignment matched, only the back side of the hand and outstretched finger were seen, whereas when the two types of compatibility did not match the images shown in that condition depicted the palm view of the hand, which had more internal visual information as all fingers were also in view.

The response time data met the sphericity assumption ($\varepsilon = 0.75$). A main effect of SOA was strong supported (*BF* > 1,000). For all other main effects and interactions the null model was supported by a Bayes factor of at least 2 (except the SOA by compatibility interaction, which favoured the null model by a factor of only 1.4). Separate analyses for each SOA revealed that at the short SOA evidence for both main effects and the interaction favoured the null by a factor of at least 4. At the long SOA the interaction was only anecdotally supported (*BF* = 1.2) whereas the evidence for both main effects favoured the null, though this support was only anecdotal for the factor of compatibility.

Percent error colour dot trials. The percent error data did not meet the sphericity assumption (ε = 0.60) so I moved to a BIC approximation of the Bayes factor. Fewer errors were made when the laterality of the depicted hand and the response hand matched (3.4%) compared to when they did not match (4.7%; *BF* = 7.9). All other main effects and interactions favoured the null model by a factor of at least 3.

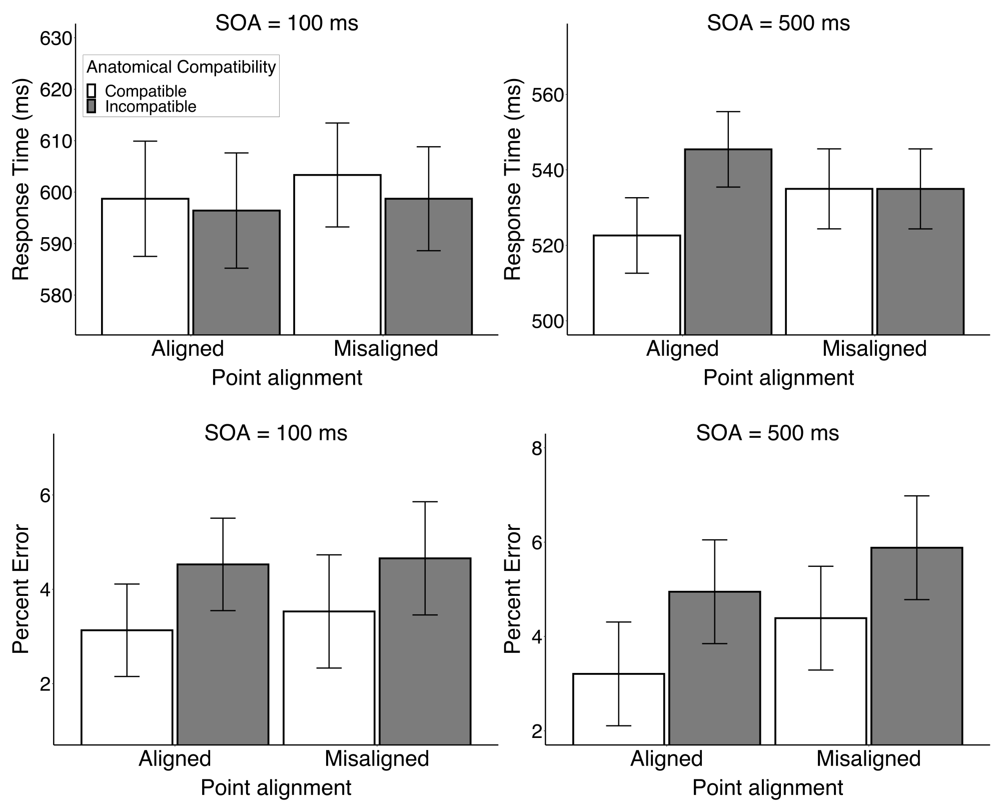

Figure 26. Mean response time and percent error in Experiment 4d as a function of SOA, alignment between the direction in which the depicted hand pointed and the response hand, and compatibility between the laterality of the hand cue and the laterality of the correct response hand on colour-dot trials.

Response time distribution. The compatibility effect size by quintile at each SOA when the point direction was aligned versus misaligned with the response is shown in Figure 27. The linear trend analyses favoured a flat interpretation of the delta plots in all cases. The mean weighted sum and Bayes factor t-test results for each condition are presented in Table 5.

Table 5. Results of linear trend analyses for Experiment 4d

SOA	Point Alignment	Mean weighted sum	Bayes Factor
100 ms	Aligned	-6.1 ms	5.5 in favour of null
100 ms	Misaligned	-9.4 ms	4.5 in favour of null
500 ms	Aligned	10.0 ms	3.8 in favour of null
500 ms	Misaligned	-6.3 ms	5.3 in favour of null

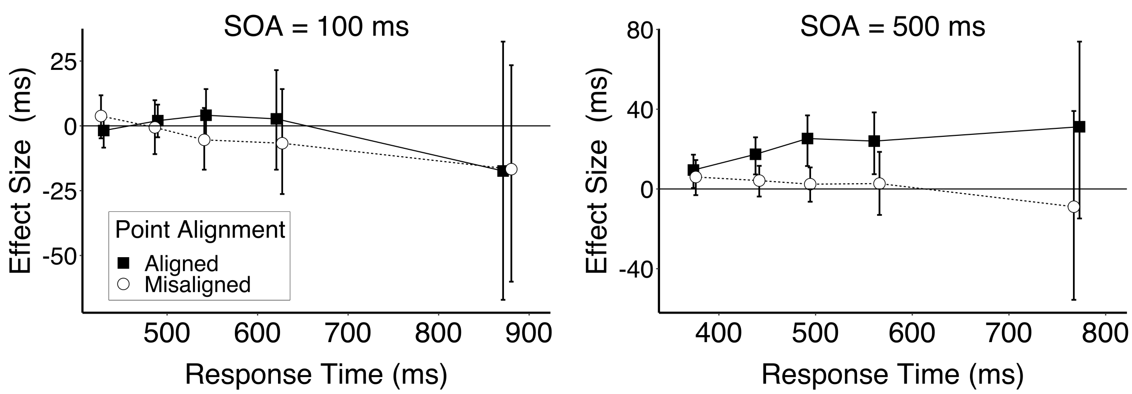

Figure 27. Response time delta plot for the compatibility effect by point alignment at each SOA in Experiment 4d.

Discussion

Introducing a laterality judgment task on a minority of trials resulted in a pattern of SRC effects produced when judging the laterality of a coloured dot superimposed on a task-irrelevant press-posture hand that was very different from the pattern of effects generated by these same stimuli in the absence of the laterality-judgment task context. The SRC effects in Experiment 4 are substantially larger in magnitude than those measured in the previous experiments. Additionally, these SRC effects are clearly effector-specific, and reflect a benefit of correspondence between the depicted and response hand laterality, compared to when they do not correspond, regardless of the location of the response key. This finding suggests that increasing attention to the laterality of a hand image encourages effector-specific coding of the stimulus, response options, or both – even on trials where an explicit laterality judgment is not made. The relative delay in the response on laterality-judgment trials compared to colour-judgment trials suggests that participants were not explicitly prejudging the laterality of each hand prior to the onset of the dot cue. This suggests that some other mechanism is responsible for producing the pattern of results obtained in Experiment 4, such as shifting the participants' frame of reference from an extrinsic/spatial to an intrinsic/body-based frame. Surprisingly, the horizontal pointing hands in Experiment 4d did not produce the same large hand compatibility effects that the press hands did. This could reflect that extracting laterality from these images was more difficult compared to the press posture images, which is supported by the lower laterality judgement accuracy in Experiment 4d (73%) compared to the press-hand experiments (mean laterality judgement accuracy = 90%). The relative difficulty of explicitly extracting laterality from the horizontally pointing images might also account for the relatively small effects of hand laterality on colour dot response times.

Experiment 5

Introduction.

Thus far I have demonstrated two task contexts in which effector-based SRC effects can be reliably elicited: (1) When participants make left/right-hand responses to a colour cue superimposed on a task-irrelevant hand in a power-grasp posture, and (2) when participants make left/right-hand responses to a colour cue superimposed on a task-irrelevant hand, and on some proportion of trials they make explicit hand-laterality judgments. I can now apply these task contexts to evaluate a contentious, yet persistent, claim made in the literature that images of handled objects automatically evoke effector-specific representations of the hand that one would use to interact with the handle of the depicted object. Bub et al. (2021) examined the way in which response cueing methods and response modes modulated handle-alignment effects. They found that when responses were made to the direction of an arrow superimposed on a whole-object centered object image, a reverse handle-alignment effect was produced. By changing the response mode to a reach-and-grasp response, rather than a keypress, the handle-alignment effect reversed – and now responses were made more quickly when the object's handle aligned with the response hand. Critically, a positive handle-alignment effect was also obtained when participants made keypress responses to the laterality of a power-grasp hand superimposed on the object, rather than an arrow. This result might be visual, arising due to stimulus-stimulus compatibility between the object's handle and the depicted hand. An alternative hypothesis is that either viewing the hand, or judging its laterality, involved a motor representation, and changed the way in which the object was encoded. Experiment 5a was designed to explore whether positive handle-alignment effects would emerge automatically when objects were presented with task-irrelevant power-grasp images. This task followed the procedure described in Experiment 1a, using stimuli depicting power-grasp hands superimposed on a teapot with either a right- or left-pointing handle (see Figure 28a). Given that a positive alignment effect was not generated under these conditions, Experiment 5b was designed to increase attention to the object (through the inclusion of a second object and probes of object identity), increase attention to the laterality of the hand (through the inclusion of laterality-judgment trials, cued by a grey dot), and increase the salience of the relationship between the hand and object by changing the hand image to one the more closely imitates the form of a hand reaching toward an object with a vertically oriented handle from an egocentric perspective (these stimuli were taken directly from Bub et al., 2021; see Figure 28B).

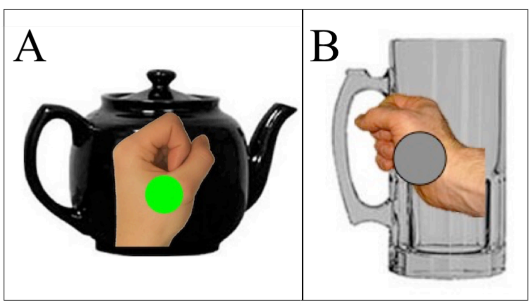

Figure 28. Sample images from Experiment 5a (panel A) and 5b (panel B).

Method

Participants. Forty-eight participants were recruited for Experiment 5a, which was a lab-based study and 60 participants were recruited for 5b, an online study. All participants in both 5a and 5b met the 80% task accuracy threshold. Experiment 5b contained additional probe questions on 25% of trials, and 3 participants were dropped for failing to meet an a priori probe accuracy threshold of 75%. The average probe accuracy for the remaining participants was 92%. An additional 9 participants were excluded from Experiment 5b (4 who indicated that they did not always follow task instructions and 5 who had a mean correct RT greater than 1,000 ms). Of the 80 participants included in Experiment 5, 59 were female, 75 were right-handed, and the median age was 22 yr (range 18 to 70 yrs).

Materials. In Experiment 5a, power-grasp hand images were superimposed on greyscale images of a teapot (see Figure 28a). The hand images were identical to those used in Experiment 1, except that the hands were presented in colour, rather than greyscale, to increase visual contrast between the object and the hand. A 345 x 240 pixel teapot image was horizontally mirrored to create both left- and right-side handle versions. Both the hand image and the teapot image were centered on a white background of 400 x 400 pixels. The left- and right-hand versions of the power grasp were each paired with a left- and right-side handle version of the teapot. This resulted in two stimulus-stimulus compatible images (e.g., a left hand with a left-handled teapot) and two stimulus-stimulus incompatible images (e.g., a left hand with a right-handled teapot). Two coloured-dot versions of each stimulus were also generated.

In Experiment 5b, images of left- and right-handled beer mugs were used in addition to the left- and right-handled teapots from Experiment 5b. Power-grasp hand images from Bub, et al., (2021) were superimposed on the images of the objects. These images depicted a power-grasp hand from an egocentric side view, rather than a top-down view, to more consistently match the view one would have on their own hand as they grasped a beer mug or teapot positioned in front of them. Left- and right-hand versions of the hand stimuli were generated, and each was superimposed on an image of both the left and right-handled versions of both objects (see Figure 28b). Three versions of each of the resulting 8 images were generated by superimposing either a purple, orange, or grey dot on the hand. The teapot images in this version of the experiment were slightly smaller to match the images used in Bub, et al. (approximately 355 x 175 pixels). The beers mug images were approximately 140 x 215 pixels, and the hand images were approximately 100 x 100 pixels. The dot was scaled down to 40 pixels in diameter to avoid obfuscating the fingers.

Procedure. The procedure of Experiment 5a was identical to Experiment 1, except that participants responded using only the straight-hand response mode. The number of critical trials was increased (320), as the number of unique trials doubled by superimposing the images on the left- or right-handled teapot.

Experiment 5b used the same procedure as Experiment 4a, in that participants made straight-hand responses to the colour of the dot on 80% of trials, and responded to the laterality of the hand prime on the remaining 20% of trials which were cued by a grey dot. On 25% of the trials of each type a probe question was presented following a keypress response. The probe question required participants to verbally indicate the identity of the object (teapot or beer mug) that was presented on that trial. The experimenter scored the probe response with a keypress, which coded the correctness of the response and triggered the experiment program to begin the 750-ms inter-stimulus-interval.

Given the relative difficulty of the task, participants began by completing 3 blocks of practice trials, 1 in which they practiced responding to only the colour of the dot (16 trials), 1 in which they practiced responding to only the laterality of the hand (8 trials), and 1 in which they practiced the full task, including making probe responses (16 trials).

The critical block contained 320 critical trials, with self-regulated rest breaks given every 64 trials.

Results

Averaging across both versions of Experiment 5, mean accuracy on the colour dot task was 97%, and ranged from 86-100% correct. Following the outlier removal procedure described in Experiment 1, response times less than 100 ms were removed from both experiments, and the upper cutoff was set at 1,000 ms and 2,200 ms for Experiments 5a and 5b, respectively. Incorrect trials were removed from the response time analysis and laterality judgment times were removed from the analysis in 5b. The average accuracy on the laterality judgment task was 95% and ranged from 62% to 100%.

Experiment 5a results

Response time. An analysis of the RT data included the factors of SOA, anatomical compatibility (between the laterality of the response hand and the depicted hand) as well as object alignment, defined as a match between the location of the object's handle and the location of the response key (which was the same as the response hand, given that participants were responding using a straight-hands response mode). The mean response times for these conditions are depicted in Figure 29. The response time data did not meet the sphericity assumption ($\varepsilon = 0.38$), so the BIC approximation procedure was used. As is standard, there was strong evidence in favour of a main effect of SOA. Consistent with my findings in Experiment 1, there was strong evidence for a main effect of anatomical compatibility ($BF = 22.4$) in which responses were made more quickly when the response-hand laterality matched the depicted-hand laterality (422 ms) compared to when they did not match (430 ms). Anatomical compatibility interacted with

SOA (*BF* = 7.0). The compatibility effect was larger at the short SOA (11 ms) than the longer SOA (3 ms). There was also positive support for a main effect of object alignment (*BF* = 4.7). This alignment effect was very small, and most interestingly it was a reverse handle-based effect. That is, responses were made more quickly when the object's handle was on the side opposite to the side of response (425 ms), compared to when the handle and response hand were aligned (427 ms). Another way to conceptualize the same result is that responses were made more quickly when the response hand was aligned with the location of the teapot’s spout. Object alignment did not interact with either anatomical compatibility (*BF* = 3.5) or SOA (*BF* = 2.3), nor was there evidence in favour of a 3-way interaction (*BF* = 6.9).

Percent error. The percent error data included the factors of SOA, anatomical compatibility and object alignment. The data did not meet the sphericity assumption (ε = 0.73), so the BIC approximation procedure was used. There was positive evidence in favour of a main effect of anatomical compatibility (*BF* = 5.2). Evidence for all other main effects and interactions favoured the null by a Bayes factor of at least 3.

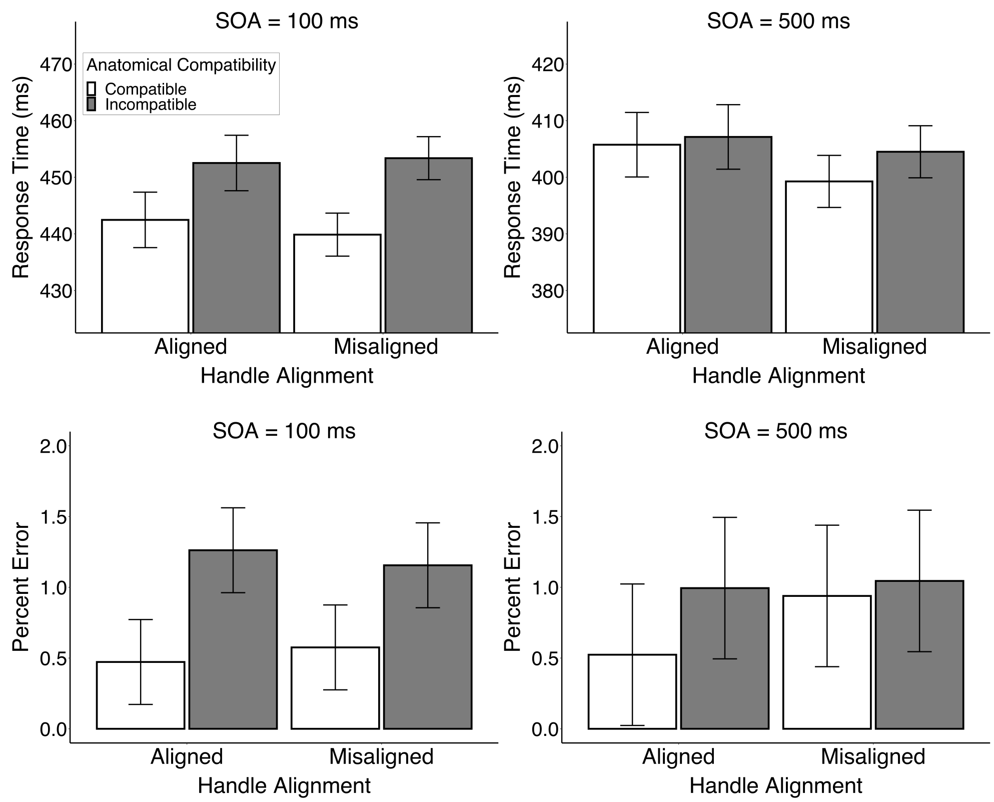

Figure 29. Mean response time and percent error in Experiment 5a as a function of SOA, alignment between the side of the handle and side of response, and compatibility between the laterality of the hand cue and the laterality of the correct response hand.

Response time distribution. The handle-alignment effect size by quintile at each SOA when the handle location was aligned or misaligned with the response location is shown in Figure 30. The linear trend analyses of the alignment effect favoured a flat function for the delta plots in all conditions. The mean weighted sum and Bayes factor t-test results for each condition are presented in Table 6.

Table 6. Results of linear trend analyses for the alignment effect in Experiment 5a.

SOA	Compatibility	Mean weighted sum	Bayes Factor
100 ms	Compatible	0.2 ms	6.3 in favour of null
100 ms	Incompatible	0.8 ms	6.2 in favour of null
500 ms	Compatible	-1.1 ms	6.0 in favour of null
500 ms	Incompatible	-8.2 ms	1.4 in favour of null

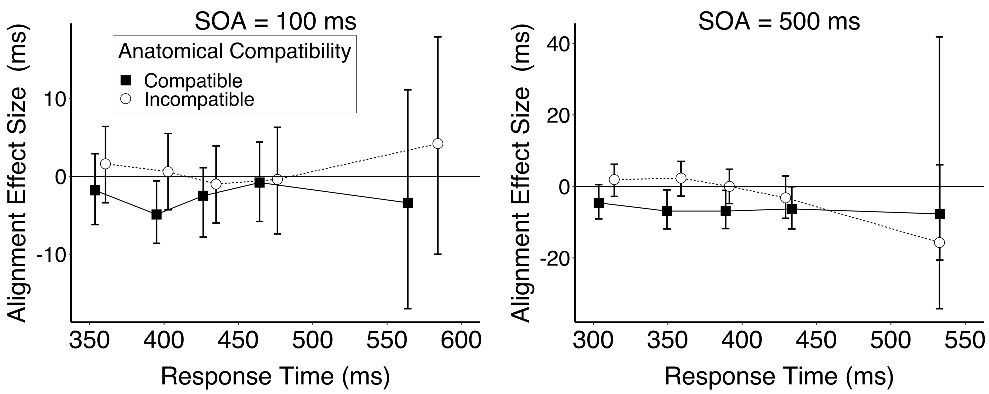

Figure 30. Response time delta plot for the handle-alignment effect in Experiment 5a by anatomical compatibility and SOA.

Experiment 5b results

Laterality judgment trials. An analysis of the laterality judgment data included only grey-dot trials and included the factors of SOA and object alignment. These time data met the sphericity assumption ($\varepsilon = 0.88$). There was very strong evidence for a main effect of SOA ($BF > 1{,}000$). Additionally, there was positive evidence in favour of a handle-alignment effect ($BF = 3.6$). The alignment effect ran in the expected positive direction. Laterality judgment responses were made more quickly when the location of the handle was aligned with the response (809 ms ; stimulus-stimulus compatible condition) then when they were not aligned (830 ms ; stimulus-stimulus incompatible). These results could be interpreted as either a positive handle-alignment SRC effect, or a positive stimulus-stimulus compatibility effect.

Colour judgment response time. An analysis of the RT data included only coloured-dot trials and included the factors of SOA, anatomical compatibility, and handle alignment (defined as alignment between the object's handle location and the response hand). The mean response times for these conditions are depicted in Figure 31. The response time data met the sphericity assumption ($\varepsilon = 0.77$). There was very strong evidence in favour of a main effect of SOA (*BF* > 1,000), as well as in favour of a main effect of anatomical compatibility (*BF* > 1,000). Responses made to the coloured dot were faster when the laterality of the response hands matched the laterality of the depicted hand (659 ms) compared to when they did not match (746 ms). Critically, the evidence for the effect of handle alignment favoured the null (*BF* = 7.4). All other interactions also favoured the null, though the evidence was merely anecdotal for the anatomical compatibility by object alignment interaction (*BF* = 1.4), as well as for the 3-way interaction (*BF* = 2.1). Separate analyses for each anatomical compatibility condition were conducted, and in each case evidence in of a handle-alignment effect favoured the null by a factor of at least 2.

A follow-up analysis was conducted to test the possibility that the null handle alignment effect was not in fact the result of two conflicting object-based spatial effects. As demonstrated in Experiment 5a, as well as by Bub, et al. (2021), a teapot can produce a spatial code consistent with the location of the object's spout, which appears as a negative handle-alignment effect. If the teapot continued to produce a negative alignment effect in Experiment 5b, and the beermug produced a positive handle alignment effect, this might give the appearance of a null effect overall. To test for this possibility, I conducted an analysis including object type (teapot or beermug), handle-alignment, and SOA as factors. The critical interactions were the object type by handle-alignment, which favoured the null anecdotally (*BF* = 1.2), and the 3-way interaction, which favoured the null (*BF* = 6.6). The mean RTs indicated that responses to the teapot were 9 ms shorted when the response hand was aligned with the handle, while for the beermug the mean RT was 8 ms longer when the response hand was aligned with the handle. The direction of these differences are the opposite of what we would have expected for each object if they were producing spatial code, but importantly, separate analyses of the handle-alignment effect for each object indicated that the null was favoured both for the teapot (*BF* = 2.7) and for the beermug (*BF* = 3.6).

Percent error. The percent error data was analyzed in the same fashion as the response time data. The data did not meet the sphericity assumption ($\varepsilon = 0.55$), so a BIC approximation was used. There was very strong evidence in favour of a main effect of anatomical compatibility (*BF* > 1,000), with fewer errors made under compatible, compared to incompatible conditions. Evidence for all other main effects and interactions favoured the null, though the evidence was merely anecdotal for the main effect of handle alignment and the anatomical compatibility by SOA interaction.

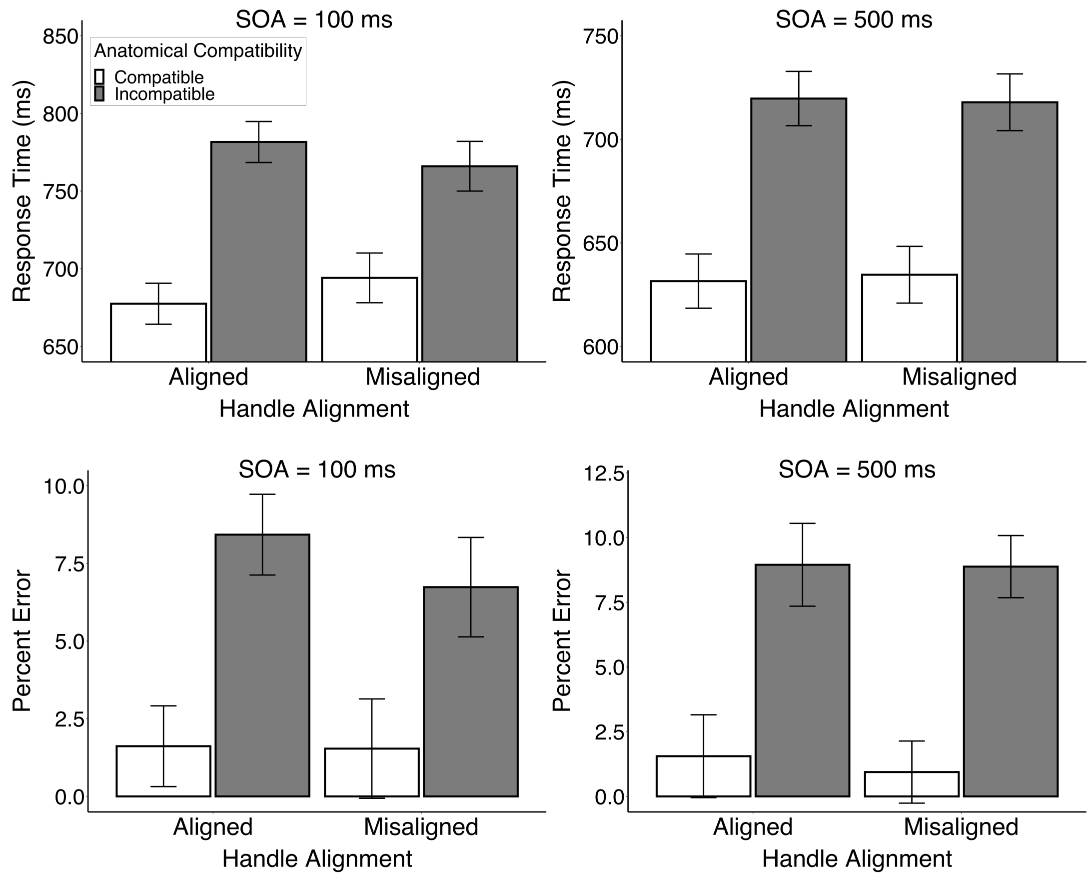

Figure 31. Mean RT and percent error on colour-judgment trials in Experiment 5b as a function of SOA, anatomical compatibility, and handle alignment.

Response time distribution. The handle-alignment effect size by quintile at each SOA when the handle location was aligned and misaligned with the response location is shown in Figure 32. The linear trend analyses of the alignment effect favoured a flat interpretation of the delta plots in all conditions, though the evidence was merely anecdotal for the incompatible-hand condition. The mean weighted sum and Bayes factor t-test results for each condition are presented in Table 7.

Table 7. Results of linear trend analyses for the alignment effect in Experiment 5b.

SOA	Compatibility	Mean weighted sum	Bayes Factor
100 ms	Compatible	10.4 ms	4.7 in favour of null
100 ms	Incompatible	11.6 ms	4.0 in favour of null
500 ms	Compatible	-7.6 ms	5.3 in favour of null

500 ms	Incompatible	-17.7 ms	1.7 in favour of null

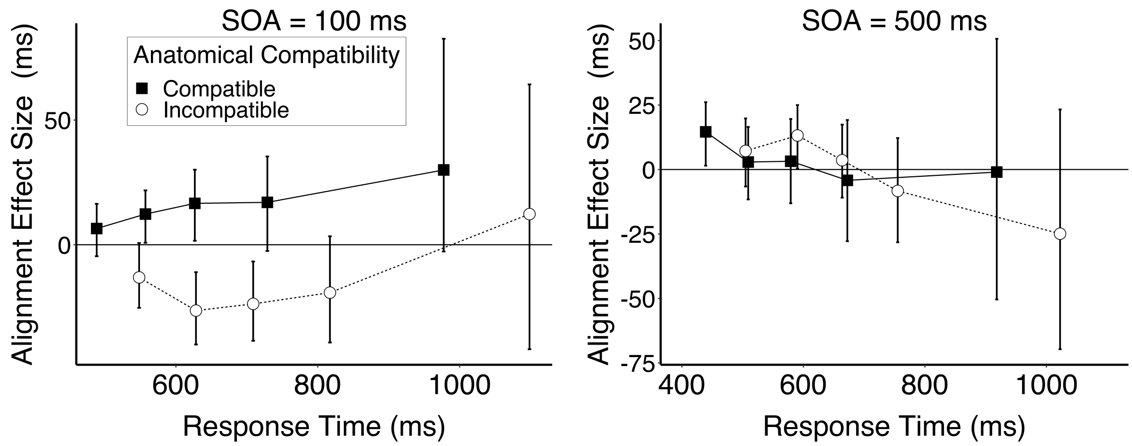

Figure 33. Response time delta plot for the handle-alignment effect in Experiment 5b by anatomical compatibility and SOA.

Discussion.

Experiment 5a made use of a colour-judgment task with left/right power-grasp images superimposed on a teapot with a left/right-handle orientation. There was a small but reliable SRC effect between the depicted hand and the response hand, consistent with the results obtained in Experiments 1 and 2. Based on the results of those earlier experiments, this effect is likely effector-specific, and reflects that the image of the hand is coded according to an intrinsic frame of reference. However, my hypothesis that within this task context the image of the teapot would be encoded in the same frame of reference was not supported by the data. Rather, the alignment effect produced between the location of the object's handle and the response location was reversed. This reverse alignment effect is similar to the result obtained by Bub et al., (2021) when participants made keypress responses to the direction of an arrow superimposed on an image of a teapot. Notably, when participants made a reach-and-grasp, rather than a keypress, response to the direction of an arrow superimposed on a teapot, a positive alignment effect between the handle location and the response hand now emerged. This suggests that when one is in a state of intending to act, an object is coded in terms of its motor, rather than its spatial properties. It is most interesting then that the same motor-like encoding of the teapot did not occur in the presence of a power-grasp hand image, which does appear to be coded in an effector-specific motor-like manner.

The results of the grey-dot trials in Experiment 5b were consistent with the results of Bub et al. (2021), in that a significant effect of object alignment was found on trials where an explicit laterality judgment response was made. These results share the same drawback as the original finding, in that this design does not allow me to determine whether this effect emerges due to alignment between the handle location and the response, or whether it reflects stimulus-stimulus compatibility, as on these trials a left-hand response is made only when a left hand is present on the screen (and thus, a trial in which the response is aligned with the handle will necessarily be a stimulus-stimulus compatible trial). The alignment and stimulus-stimulus compatibility effects are decoupled on the colour-dot trials in this task, as now each stimulus-stimulus pair is combined with a colour dot that cues either a left or right response.

The colour-dot trials in Experiment 5b showed a clear anatomical compatibility effect, as expected. In terms of magnitude, this compatibility effect is by far the largest seen across the experiments reported in this manuscript- including other experiments which made use of the grey dot. This might be due to some visual property of the hand stimulus, which has not been examined under any other task conditions. It is also a possibility that some feature of the task demands (such as the split attention between the dot task and the task to report on object identity) boosted the effect of the hand prime on response. In any case, even when this particular power-grasp posture was presented with an object under these task conditions there was no evidence in support of a main effect of handle alignment or an interaction between handle alignment and anatomical compatibility. This, taken together with the null alignment effect in Experiment 5a, suggests that the mechanism responsible for producing handle-alignment effects like those seen on the grey-dot trials in Experiment 5b and those reported by Bub et al (2021) is reliant on an explicit laterality judgment being made – and simple attention to hand laterality is not sufficient for producing these effects. This finding is particularly interesting in the context of Experiments 3 and 4, which demonstrated that adding laterality judgment trials was sufficient for boosting the anatomical SRC effect for press hand images. It appears that whatever state participants are in during tasks that include grey and colour cues is not the same as the state involved when explicitly judging laterality, or when forming an action intention or action plan to make a reach-and-grasp action.

General Discussion

The work presented in this dissertation contributes to an increasingly unified understanding of the way in which task-irrelevant hand primes influence manual responses in a stimulus-response compatibility paradigm. Where earlier accounts proposed that hand images automatically generated only extrinsic spatial codes (Ottoboni et al., 2005), only effector-based codes (Vainio and Mustonen 2011), or simultaneous spatial and effector-based codes (Nishimura and Michimata, 2013), I propose that hand images can be represented in either an effector-specific or a spatial manner, and that the nature of the representation generated by a hand image is determined by both stimulus properties and task context.

The role of stimulus properties

The results of Experiments 1 and 2 provide converging evidence in support of the claim that task-irrelevant images of power-grasp hands reliably generate SRC effects that are effector-specific in nature. That is, a hand image primed a key-press response on the basis of a relationship between the prime and response hand identity, rather than a relationship between the prime hand and the location of the response key. Key evidence for this effector-based relationship was obtained by comparing the SRC effects generated under straight hand and crossed hand response modes, which shows that a left hand response on either a left or right-sided key are made more quickly when primed by an egocentric left hand, compared to an egocentric right hand (and egocentric right hands primed faster right-handed responses). When hands are presented from an allocentric perspective the direction of the effect reverses (e.g., a left hand primes a faster right hand response). As evidenced by the crossed hands condition, this effect is still based on the identity of the response hand, and not the location of the response key. Effector-based effects also emerged when responses were made using vertically oriented keys. The presence of effector-based SRC effects under these conditions demonstrates that coding response keys according to a left/right spatial dimension is not required to generate left/right lateralized response codes. Finally, when participants responded using two fingers of their dominant hand, a reliable SRC effect was not produced. Together, these findings provide clear evidence for the claim that power-grasp hand images are coded according to a body-based/ intrinsic frame of reference, in which the laterality of the depicted hand is mapped to a particular response hand.

Given this evidence that power-grasp hand images automatically generate effector-based SRC effects, it would not seem unreasonable to hypothesize that hand images in general are coded according to a body-based frame of reference. It is perhaps the most striking finding reported in this dissertation that a simple change in the depicted hand posture — from a clenched fist to a slightly rotated fist with an extended thumb and index finger — dramatically and reliably changed the way in which the hand images were coded under identical task conditions. These so-called press-posture hands generated spatial SRC effects, on the basis of compatibility between the depicted hand and the location of the response key (not the laterality of the response hand). Further, the dimension of the hand prime that was relevant to this relationship was not it’s identity- but rather the location of the outstretched fingers, as evidenced by the comparisons between the palm and back view of the hands in Experiments 3a and 3b. Even when response keys were oriented vertically, which removed the possibility of coding the response keys in terms of their left/right spatial dimension, an effector-based SRC effect did not emerge for press-posture hands, the way that it did for power-grasp hands. This suggests that under these task conditions, press-posture hands are coded only in terms of their visuospatial, and not motor, properties.

This evidence that hand posture plays a key-role in determining the nature of the representation evoked by a hand image appears to contradict results obtained by Vainio and Mustonen (2011). They report positive SRC effects generated by both power-grasp and press-posture hand images. There are a number of methodological differences between the present work and Vainio and Mustonen's that could potentially account for these diverging results. For example, Vainio and Mustonen utilized spatial cues, removed the cue after a 200 ms presentation time, and randomly intermixed mixed hand postures within a single study- while the present work utilized non-spatial cues that remained in view until response and did not intermix hand postures. It would be valuable for future work to determine which methodological factor(s) is responsible for generating these differences in the SRC effects. However, even without this knowledge, it is clear that Vainio and Mustonen's assertion that hand posture does not influence the way in which the stimulus is mapped to the response is not consistent with the evidence presented here. Rather, it is apparent that visuospatial properties of the hand image influence the way in which task-irrelevant hand primes are encoded, and the way in which manual key-press responses are generated.

Nishimura and Michimata (2013) proposed that hand stimuli could generate spatial as well as effector-specific SRC effects when the cue was presented at a 560 ms SOA. However, distinct from my assertion, they claimed that both representations could be evoked by a single hand image, simultaneously. This claim is not consistent with the data here, which does not show any indication that press-posture hands generate both spatial and effector-based codes within a single task. If it were the case that both types of representations were evoked, I would expect evidence of two competing effects for back-view stimuli, and two additive effects for palm-view stimuli. This could take the form of overall larger effects for palm-view hands compared to back view hands, which is not consistent with the evidence from Experiments 3a and 3b. Alternatively, I would expect to see evidence of a quickly emerging effector-based SRC effect and a slower developing spatial-based SRC effect if both spatial and effector-based representations were present. For palm-view hands, this might appear as a reliable effect at the short SOA that grows further by the long SOA, and a null or reverse (in this case, a positive anatomical compatibility effect) for back-view hands at the short SOA that grew to a spatial (or a negative anatomical compatibility effect) effect at the longer SOA. Again, this is not consistent with the evidence found in Experiments 3a and 3b. If anything, Experiment 3a shows that the effect takes longer to emerge for the palm-view than the back-view hands, which is inconsistent with this prediction. Further, we see in the delta plots for Experiments 3a and 3b that even at the fastest quintiles there is no evidence that back-view hands are generating an effector-based SRC effect. This evidence is not compatible with the claim that spatial and effector-based effects are both evoked by the hand images. I concede that press-posture stimuli I used were different from the horizontally pointing hand images utilized by Nishimura and Michimata, however it seems a fair assumption that their stimuli were more strongly spatial than the press-posture images, and therefore it is not clear why horizontally pointing hands, but not press hands, would generate effector-based representations. Given the very small size of not only the effector-based (5 ms) but also the spatial-based (6 ms) effects reported by Nishimura and Michimata, it would be worth determining if their results were reproducible before making an effort to include these results in a unified account of the nature of representations automatically evoked by hand images. As it stands, the clearest evidence regarding the way in which hands with salient spatial asymmetries are encoded is reported in the present work, and this evidence suggests that visual properties of a task-irrelevant hand image appear to influence the way in which the stimuli are represented by influencing the selection of a single reference frame (intrinsic/spatial or extrinsic/effector-based) in which the stimuli are coded.

The role of task context

Experiments 1-3 clearly established that under task conditions in which power-grasp hands generated effector-specific SRC effects that were based on the depicted hand's laterality, press-posture hand images instead generated spatial SRC effects based on the location of the extended forefinger and thumb. In Experiment 4, I demonstrated that by changing the context of the task, these press-posture hands could instead be coded in an effector-specific manner based on their left/right identity. Namely, by intermixing trials in which hand laterality was a task-relevant dimension with standard trials in which hand laterality was not task-relevant, effector-specific SRC effects emerged when participants made colour judgements of dots superimposed on press-posture hand primes.

There are a few possible ways in which adding laterality judgement trials might have changed the way in which the hand prime was encoded on colour dot trials. For example, participants might have paid more attention to the hand prior to the onset of the cue before it was known if the hand's laterality would be task relevant or not. Recall

Parson's (1994) model of hand representations, which posits that in the context of ultimately judging the laterality of a hand image, laterality information is preattentively extracted from the image. This rapid identification of the hand's identity is not sufficient for making an explicit laterality judgement, but rather it allows the viewer to reference the motor representation of their own hand of corresponding laterality. It is possible that adding laterality judgement trials to the task context encouraged this process of identification and consultation of a motor representation to begin upon onset of the hand image. In this way, the change in task context (inclusion of laterality judgement trials), may have changed the evoked representation (motor, rather than spatial), by priming a motor representation which became dominant over a simple spatial representation based on visual asymmetries of the image.

An alternative explanation for how adding laterality-judgement trials might have influenced the nature of the hand representation is that these trials changed the way in which the response options were coded, which could in turn prime the viewer to code the hand differently as well. Most visual SRC effects reflect extrinsic coding between the stimulus properties and response keys. A notable exception is the SRC effects evoked by power grasp hands in Experiments 1 and 2, which show that the response options are coded as left/right hands, not keys. This exception seems to suggest that an effector-based coding occurs when 1) the stimulus can easily/directly be mapped to an effector and 2) the stimulus lacks any salient spatial dimension. As soon as either of these conditions is not met, the response options appear to default to a key-based, rather than effector-based, mapping. I suggest that the inclusion of the laterality-judgment trials could cause participants to code the response options by effector, and that this mapping was used for the entirety of the task, including on colour-judgement trials. I propose that changing the way the response options were coded from an extrinsic to an intrinsic reference frame primed the way that the stimulus was coded as well- from a spatial stimulus to a representation of a particular effector. This hypothesis relies upon the assumption that within a task, subjects are unable to code a hand according to two reference frames, simultaneously, which is consistent with the evidence presented in this thesis and with work examining mixed-modality SRC effects (Ruzzoli & Soto-Faraco, 2017; but see above for how this evidence conflicts with the findings of Nishimura and Michimata, 2013).

Though I have presented evidence that an image of a hand alone is coded according to either its visuospatial or limb-specific properties (but not both at the same time), I have also shown that a hand presented in conjunction with the image of a handled object is capable of generating two types of representations, one of the hand, and one of the object. Experiment 5a shows clear hand-based effects are evoked by a power grasp image, while at the same time a small spatial alignment effect is evoked by an image of a teapot, which suggests that the two elements of the image are being coded according to two different reference frames, simultaneously. This is a most interesting finding, given that there are many who claim that the image of a handled object itself is capable of generating motor-based representations corresponding to the would-be-acting hand of the observer (e.g., Tucker & Ellis, 1998; Pappas, 2014). Here, I show that even under conditions, which should strongly encourage motor-based coding of the object image, the object generated only spatial SRC effects. This implies that the image of a hand on an object is not processed as a gestalt in terms of the potential motor properties of the object, but as an image with two wholly separate components. Consistent with the findings of Bub et al., (2021), when laterality-judgment trials were added to the experiment a handle-based alignment effect of the teapot and beermug emerged. But critically, this effect was isolated to the laterality judgment trials, and did not "spill over" on to the colour judgment trials in this task. This suggests that there is something special about the influence of making an *explicit* laterality judgement of a hand presented with a handled object that encourages an effector-based coding of the object image, which is not present simply due to coding the hand in an intrinsic frame of reference or paying attention to the hand image. This lends further support to the theory that images of handled objects do not automatically evoke associated motor representations of the actions that they are said to afford, but that such representations can be evoked in particular circumstances based on the viewer's motor intentions/planning (Bub et al., 2021; Bub & Masson, 2010; Bub, Masson, & Kumar, 2018). It also suggests that an image of a hand is coded according to a single reference frame not because we are incapable of applying two reference frames to a stimulus simultaneously, but rather because a hand image on its own cannot be represented as duality of its structural and effector-based components.

Conclusions

In summary, this work shows that the nature of a representation automatically evoked by an image of a hand in a stimulus-response paradigm is determined by both features of the stimulus itself, as well as properties of the task context. Images of hands with salient visuospatial asymmetries appear to be coded according to a reference frame that is extrinsic to the body, unless a task context is introduced which primes the use of an intrinsic reference frame, which leads to effector-based coding of the hand stimuli. On the other hand, power grasp hand images (which are relatively symmetrical), automatically and rapidly evoke effector-specific representations of the corresponding response hand.

Within the larger context of the work investigating the relationship between visual representations and the motor system, this work shows that even under ideal conditions in which static images might automatically evoke motor representations, visuospatial features of the image can, in some contexts, be dominant over effector-based representations. These findings, which show that even some hand images do not necessarily evoke motor representations of the viewer's own hands, should cast further doubt upon the widespread expectation in the embodied cognition literature that static images automatically evoke associated motor representations.

References

Ariga, A., & Watanabe, K. (2009). What is special about the index finger?: The index finger advantage in manipulating reflexive attentional shift 1. *Japanese Psychological Research*, *51*(4), 258-265.

Bracci, S., Caramazza, A., & Peelen, M. V. (2018). View-invariant representation of hand postures in the human lateral occipitotemporal cortex. *NeuroImage*, *181*, 446-452.

Bracci, S., Ietswaart, M., Peelen, M. V., & Cavina-Pratesi, C. (2010). Dissociable neural responses to hands and non-hand body parts in human left extrastriate visual cortex. *Journal of Neurophysiology*, *103*, 3389-3397.

Bub, D. N., & Masson, M. E. (2010). Grasping beer mugs: on the dynamics of alignment effects induced by handled objects. *Journal of Experimental Psychology: Human Perception and Performance*, *36*, 341-358.

Bub, D. N., Masson, M. E., & Kumar, R. (2018). Time course of motor affordances evoked by pictured objects and words. *Journal of Experimental Psychology: Human Perception and Performance*, *44*, 53-68.

Bub, D. N., Masson, M. E., & van Noordenne, M. (2021). Motor representations evoked by objects under varying action intentions. *Journal of Experimental Psychology: Human Perception and Performance*, *47*, 53-80.

Cho, D. T., & Proctor, R. W. (2011). Correspondence effects for objects with opposing left and right protrusions. *Journal of Experimental Psychology: Human Perception and Performance, 37*, 737-749.

Colby, C. L. (1998). Action-oriented spatial reference frames in cortex. *Neuron, 20*, 15–24.

Craft, J. L., & Simon, J. R. (1970). Processing symbolic information from a visual display: Interference from an irrelevant directional cue. *Journal of Experimental Psychology, 83* (3, Pt.1), 415–420. https://doi.org/10.1037/h0028843

de Lange, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: an fMRI study. *Neuroimage*, *33*, 609-617.

Gentilucci, M., Benuzzi, F., Bertolani, L., Daprati, E., & Gangitano, M. (2000). Recognising a hand by grasp. *Cognitive Brain Research*, *9*, 125-135.

Goodale, M. A. (2011). Transforming vision into action. *Vision research*, *51*, 1567-1587.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. Trends in Neurosciences, 15, 20–25.

Gutteling, T. P., Petridou, N., Dumoulin, S. O., Harvey, B. M., Aarnoutse, E. J., Kenemans, J. L., & Neggers, S. F. (2015). Action preparation shapes processing in early visual cortex. *Journal of Neuroscience*, *35*, 6472-6480.

Hommel, B. (1993). Inverting the Simon effect by intention. *Psychological Research*, *55*, 270-279.

Kornblum, S. (1994). The way irrelevant dimensions are processed depends on what they overlap with: The case of Stroop-and Simon-like stimuli. *Psychological research*, *56*, 130-135.

Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis of stimulus–response compatibility—A model and taxonomy. *Psychological Review, 97*, 253−270.

Lu, C., Proctor, R.W. (1995). The influence of irrelevant location information on performance: A review of the Simon and spatial Stroop effects. *Psychonomic Bulletin & Review 2*, 174–207. https://doi-org.ezproxy.library.uvic.ca/10.3758/BF03210959

Masson, M. E. (2011). A tutorial on a practical Bayesian alternative to null-hypothesis significance testing. *Behavior research methods*, *43*(3), 679-690.

Medina, J., McCloskey, M., Coslett, H., & Rapp, B. (2014). Somatotopic representation of location: evidence from the Simon effect. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(6), 2131-2142.

Nico, D., Daprati, E., Rigal, F., Parsons, L., & Sirigu, A. (2004). Left and right hand recognition in upper limb amputees. *Brain*, *127*, 120-132.

Nishimura, A., & Michimata, C. (2013). Pointing hand stimuli induce spatial compatibility effects and effector priming. *Frontiers in psychology*, *4*, 219.

Ottoboni, G., Tessari, A., Cubelli, R., & Umiltà, C. (2005). Is handedness recognition automatic? A study using a Simon-like paradigm. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 778-789.

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of experimental Psychology: Human perception and Performance*, *20*, 709-730.

Phillips, J. C., & Ward, R. (2002). SR correspondence effects of irrelevant visual affordance: Time course and specificity of response activation. *Visual cognition*, *9*, 540-558.

Pratte, M. S., Rouder, J. N., Morey, R. D., & Feng, C. (2010). Exploring the differences in distributional properties between Stroop and Simon effects using delta plots. *Attention, Perception, & Psychophysics*, *72*(7), 2013-2025.

Proctor, R. W., & Miles, J. D. (2014). Does the concept of affordance add anything to explanations of stimulus–response compatibility effects?. In *Psychology of learning and motivation* (Vol. 60, pp. 227-266). Academic Press.

Proctor, R. W., Miles, J. D., & Baroni, G. (2011). Reaction time distribution analysis of spatial correspondence effects. *Psychonomic bulletin & review*, *18*(2), 242-266.

Raftery, A. E. (1995). Bayesian model selection in social research. In P. V. Marsden (Ed.), Sociological methodology 1995 (pp. 111–196). Cambridge, MA: Blackwell.

Riggio, L., de Gonzaga Gawryszewski, L., & Umiltà, C. (1986). What is crossed in crossed-hand effects?. *Acta Psychologica*, *62*, 89-100.

Rouder, J. N., Morey, R. D., Verhagen, J., Swagman, A. R., & Wagenmakers, E.-J. (2017). Bayesian analysis of factorial designs. Psychological Methods, 22, 304–321. http://dx.doi.org/10.1037/met0000057

Ruzzoli, M., & Soto-Faraco, S. (2017). Modality-switching in the Simon task: The clash of reference frames. *Journal of Experimental Psychology: General*, *146*, 1478-1497.

Simon, J. R. (1969). Reactions toward the source of stimulation. *Journal of experimental psychology*, *81*(1), 174.

Shmuelof, L., & Zohary, E. (2008). Mirror-image representation of action in the anterior parietal cortex. *Nature neuroscience*, *11*, 1267-1269.

Taylor, A., Flynn, M., Edmonds, C. J., & Gardner, M. R. (2016). Observed bodies generate object-based spatial codes. *Acta psychologica*, *169*, 71-78.

Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human perception and performance*, *24*, 830-846.

Ulrich, R., & Miller, J. (1994). Effects of truncation on reaction time analysis. Journal of Experimental Psychology: General, 123, 34–80. http://dx.doi.org/10.1037/0096 3445.123.1.34

Ullrich, E. (2020). *An exploration of limb-specific and spatial codes triggered by pictures of graspable objects* [Unplublished Master's Thesis]. University of Victoria.

Umiltà, C., & Liotti, M. (1987). Egocentric and relative spatial codes in SR compatibility. *Psychological research*, *49*, 81-90.

Vainio, L., & Mustonen, T. (2011). Mapping the identity of a viewed hand in the motor system: Evidence from stimulus–response compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 207-221.

Wagenmakers, E. J. (2007). A practical solution to the pervasive problems ofp values. *Psychonomic bulletin & review*, *14*(5), 779-804.

Wallace, R. J. (1971). SR compatibility and the idea of a response code. *Journal of experimental psychology*, *88*, 354-360.

Zorzi, M., & Umiltà, C. (1995). A computational model of the Simon effect. *Psychological Research, 58*, 193−205.